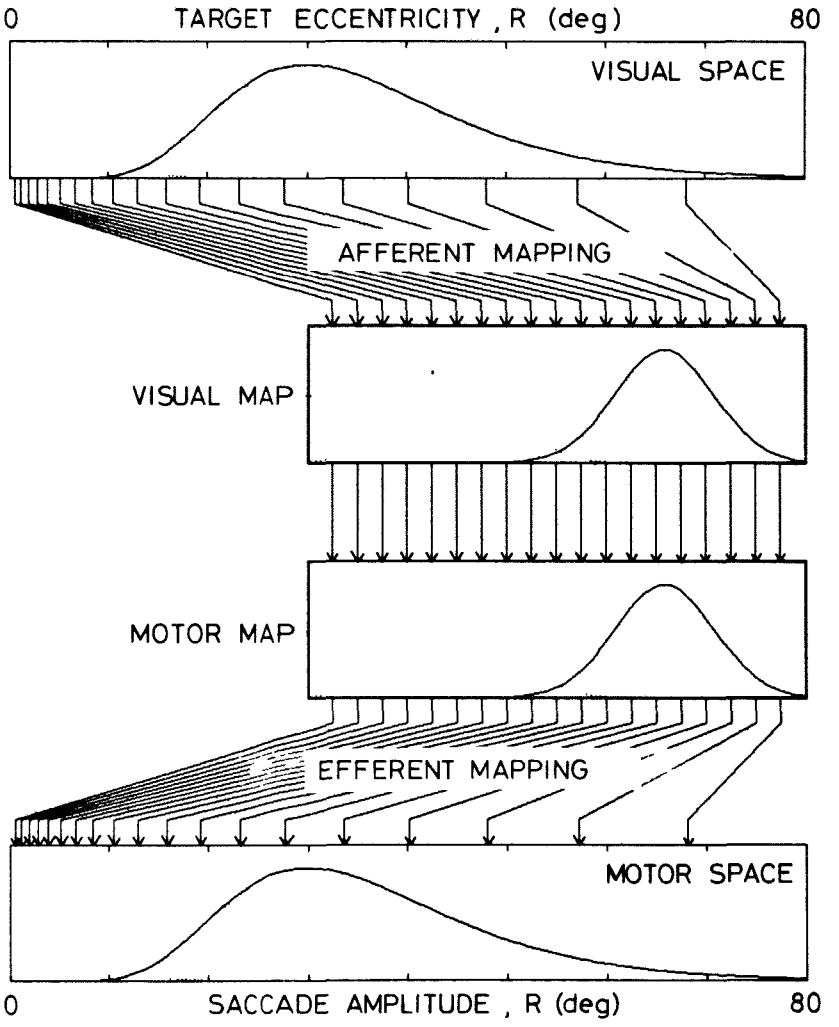
SACCADE EYE MOVEMENT RESPONSES TO VISUAL TARGET/NONTARGET STIMULI IN MAN AND MONKEY



Fenno Ottes

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Cover illustration:

General lay-out of the Superior Colliculus model described in Chapter III. In our model optic nerve fibers form an equidistant array as they enter the colliculus, but not on their points of origin on the retina, thus the resulting visual map is nonhomogeneous. When a given SC cell receives inputs from the matrix of retinal afferents according to a Gaussian connectivity function (two curves in VISUAL MAP box), its visual field will be skewed (see two corresponding curves in VISUAL SPACE box). Since, in the model, the connectivity function is spatially invariant, the curves in the VISUAL MAP box can also be interpreted as the spatial activity profile in the population of cells created by a visual point stimulus at the corresponding position on the retina (see text). When a target leads to a saccade, the movement-related activity in the model has again a Gaussian spatial distribution centered around the same mapping column (see MOTOR MAP box). The efferent-mapping function gives the relation between the location of the recruited population of movement cells and the metrics of the resulting saccade. The lines in the figure which symbolize this nonhomogeneous topographical relationship should not be interpreted as indicating anatomical connections. The skewness and the size of movement fields (see two curves in MOTOR SPACE) is determined by the Gaussian activity profile and the efferent mapping. (The scheme is part of Figure 1 in Chapter III).

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CONTENTS:

GENERAL INTRODUCTION

This thesis communicates a number of investigations on the neural generation of rapid eye movements, called saccades. This type of eye movements is used to explore any daily-life stationary visual scene, like to read this page. When a human is instructed to follow the visual stimulus or a monkey has been trained to perform that task, saccades can be elicited in these subjects by a stepwise displacement of the target from the central fixated position toward the periphery of the retina. To study the saccadic system, in this thesis two different strategies have been used. In behavioural experiments the system was investigated using a black-box approach (Chapters I and II). In electrophysiological experiments, with the application of similar conditions as in the behavioural studies, recordings were taken from single units in the superior colliculus of the alert rhesus monkey (Chapters III and IV).

As an introduction to this thesis the literature on the saccadic system will now be reviewed briefly. The motor part of the saccadic system, defined here as exclusively involved in the neural generation of the command signal for the execution of the saccade and not in the processing of the visual stimulus, will be treated first. This will be followed by a discussion of the superior colliculus and its visuo-motor functions. The main articles relevant for this thesis are named in the text. Other references can be found in recent review articles (Fuchs et al., 1985; Robinson, 1981; Schiller, 1984; Sparks and Pollack, 1976; Wurtz and Albano, 1980).

I. The motor part of the saccadic system will be described starting from the eye muscles at the periphery and moving centrally into the nervous system. The eye can be rotated through a combined action of its six external eye muscles. Each eye muscle is innervated by a pool of oculomotor neurons. The discharge rate of agonist muscle motoneurons increases, for each change in fixation position, proportionally to the difference in gaze angle along the pulling direction of the corresponding muscle. The extra static muscle force, caused by this rate increase, is required to hold the eye in its new position; it opposes the extra elastic force resulting from the change in gaze direction. The oculomotor neurons innervating the antagonist muscle show a corresponding decrease in firing rate. During the rotation of the eye a dynamic force, proportional to eye velocity is required, in addition, to overcome the viscous impedance of the oculo-motor plant, which is formed by the total aggregate of eyeball, muscles, optic nerve and other tissues in the socket. This force is created by a burst of action potentials in the agonist motoneurons and a pause in antagonist motoneurons. Thus, the execution of a saccade is accompanied by a pulse-step pattern of firing rate in the motor neurons innervating the muscles that produce the eye movement. Also each eye accelaration has found to be related to an extra, relatively small, component of the motoneuron's firing rate. This reflects the inertia of the eyeball. In accordance, it has been found experimentally that the relation between the firing rate R_m in an individual motoneuron after a small delay τ and eye position E, velocity $\dot{E}$ and accelaration $\ddot{E}$ can be described by the equation:

$$R_m(t-\tau) = R_o + k\,E(t) + r\,\dot{E}(t) + m\,\ddot{E}(t) \qquad (1)$$

where the values of the elasticity k, the damping r, the inertia m and the background firing rate at the primary position R_o are different for each neuron. To be able to investigate the behaviour of the oculomotor plant, that is to study the eye rotation in response to an innervation of the muscles by motoneuron pool activity, some assumptions have to be made. Firstly, the activity of the entire motoneuron pool can be approximated by the firing rate of a typical neuron. Further, the six eye muscles form three antagonistic pairs, in which the two muscles of each pair pull in opposite directions. Now, ignoring the background firing rate R_o, it is possible to apply system theory on the oculomotor plant and to derive the transfer function of each muscle pair by a Laplace-transformation on equation (1):

$$G(s) = \frac{E(s)}{\Delta R_m(s)} = \frac{(1/k)\,e^{-s\tau}}{(sT_{e_1}+1)(sT_{e_2}+1)} \qquad (2)$$

where G(s) is a complex function, T_{e_1} and T_{e_2}

are time constants, s represents complex frequency and the numerator term $e^{-s\tau}$ is the Laplace transform of a pure time delay τ. E(s) is the Laplace transform of eye position, and $\Delta R_m(s)$ that of the difference in firing rate between a typical agonist and antagonist motoneuron.

It has been reported that oculomotor neurons receive their inputs from so-called medium-lead burster (MLB) neurons in the brainstem. The MLBs which discharge during horizontal saccades are located in the paramedian pontine reticular formation and those firing during vertical saccades are found in the mesencephalic reticular formation. Some characteristics of the discharge patterns of these neurons are nicely related to features of the saccade. Firstly, except for small saccades, burst duration is linearly related to saccade duration. Secondly, peak firing rate is a stable function of saccade peak velocity. For saccades shorter than 10 deg this function is linear, for larger saccades it saturates. Thirdly, the number of spikes in the burst is tightly related to saccade amplitude.

Since these MLBs only carry the saccadic velocity related burst, the oculomotor neurons are thought to receive their position related step signal from another group of cells which has been found in the brainstem, namely the tonic neurons. This tonic signal is suggested to be generated by a hypothetical neural integration of the burst signal in the MLBs.

A third type of brainstem neuron, whose activity is related to the execution of saccades, is the omnipause neuron (OPN). These cells fire at a constant rate during fixation or smooth eye movements, but cease discharging completely during saccades in any direction. Since electrical stimulation near the OPNs, or pause cells for short, eliminates saccades for the duration of the stimulation, it has been suggested that these cells inhibit burst neurons.

Robinson (1981) has proposed a model for the generation of saccades in which all of the above types of brainstem neurons have a function. In the model, each saccade is initiated by an interruption of the constant firing rate in the pause cells. MLBs, normally inhibited by the pause cells, start to drive the motoneurons. Since the firing rate of MLBs has been found to decrease along a fixed alinearity as a function of actual remaining motor error independent of saccade size, it has been proposed that they are driven by an internal feedback loop. The eye position signal in the tonic cells, obtained by integration of the velocity related MLB code is substracted from the desired saccade amplitude signal and this instantaneous motor error signal is the input for the MLBs. Thus, as soon as the internal eye position signal equals the desired saccade amplitude, this input becomes zero, the MLBs are turned off, and the saccade stops.

However, this model does not include another type of brainstem neuron, the long-lead burster (LLB), which starts firing some time before the MLBs. Since monosynaptical connections have been demonstrated between the colliculus and the LLB cells, and only di- or polysynaptical connections between the colliculus and the MLBs, it has been suggested that the LLBs are interconnecting the collicular movement-related cells (see later in this section) with the MLBs. The movement-related cells in the superior colliculus code the endpoint of the ensuing saccade spatially, by way of the location of the area of neural activity within the layer where these cells reside. A typical MLB, on the other hand, codes the full velocity profile of the saccade temporally, by the course of its discharge. Several models on the neural process of spatio-temporal translation needed between the collicular movement cells and the MLBs, have been proposed.

II. The superior colliculus (SC) consists of seven alternating fiber and cell layers. Based on lesion studies, morphological distinctions between the cells, different efferent connections and the modalities of the sensory input, it has been suggested that a subdivision can be made between the superficial, intermediate and deep layers. The latter two together are often called the deeper layers. Because anatomical connections between the upper and lower part of the colliculus have never been demonstrated histologically, the superficial and deeper layers shall be treated separately in this review.

The superficial SC layers receive a prom-

inent visual projection directly from both retinae. Each cell discharges transiently after the presentation of a stimulus in a limited part of the field of view, its receptive field. The size of the receptive field increases with the anatomical depth of the cell and with the retinal eccentricity of its center. The discharge strength does not depend selectively on stimulus shape, orientation, movement direction or speed. Generally the cells fire after the onset as well as after the offset of a visual stimulus presentation. The superficial cell layer of each colliculus represents the contralateral half of the visual field in an orderly manner. The central part of the retina is represented roughly anteriorly, the periphery along the horizontal axis posteriorly. Superficial layer cells which respond optimally to stimuli in the upper part of the halffield are located medially in the SC, those with their receptive field in the lower part are situated at the lateral side of the SC. The perifoveal part of the retina is strongly overrepresented in the collicular map in comparison with the more peripheral part of the retina; the central visual field until 5 deg eccentricity covers 30% of the collicular surface in the monkey.

One class of retinal ganglion cells in the monkey has colour-opponent properties. This type of cell has opposite response patterns to different spectral stimuli. For example, a green/red colour-opponent cell may increase its firing in response to a green stimulus presentation, and show a decrease in response to a red stimulus. The colour-opponent ganglion cells project exclusively to the lateral geniculate nucleus and not to the SC. In conformity with this, it has been observed that the visual cells in the superficial layers only show colour non-opponent activity.

Some superficial cells respond more vigorously to a visual stimulus when a saccade is made to this stimulus. This enhancement of the visual response only occurs prior to a saccade in the direction of a stimulus in the cell's receptive field. If the eye jumps to a stimulus simultaneously presented remote from the receptive field, the enhancement is not observed. Each daily-life visual scene contains many features of interest which could be foveated, but since the eye can move only in one direction at once, a selection, which stimulus should be chosen as a target for a saccade, is necessary. It has been suggested that the visual enhancement is correlated with this process of selection (Wurtz et al., 1980). To investigate whether enhancement as measured in the SC contributes to target selection, when the task is more complex, is one of the reasons why target/nontarget stimuli were used during the behavioural and electrophysiological experiments in this thesis (Chapters II and IV).

The cells in the deeper SC layers show motor-related activity, that is, they discharge just before and during saccades made to visual targets. Most cells also fire if saccades are made spontaneously in the dark. The onset of the discharge generally leads the oeginning of the saccade by about 50-150 msec. Each cell only fires before saccades ending in a limited part of the visual field; this area is called the movement field of that cell. The cell's discharge is only related to the size and direction of the saccade, independent from where it started. Like visual activity, also movement-related activity shows a gradient in its vigour if the saccade vector changes across the movement field. Some neurons in the deeper layers are also visually responsive, they have larger receptive fields than neurons above them in the superficial layers.

Electrical stimulation in the SC evokes contralateral saccades, whose vector depends upon the site of stimulation within the colliculus. Stimulation thresholds are much smaller in the deeper layers than in the superficial layers. The saccade latency after stimulation is 20 msec or longer. A map of amplitudes and directions of elicited saccades has been published and this motor map was found to be in register with the sensory map existing in the superficial layers. The saccades produced by electrical stimulation had the same amplitude and direction as the sacccades for which a cell recorded at the same collicular site, discharged optimally.

Another type of collicular cells, the quasi-visual (QV) cell, is neither visual nor movement-related in the normal sense. It discharges after visual stimulation, but also prior to saccades with metrics corresponding to

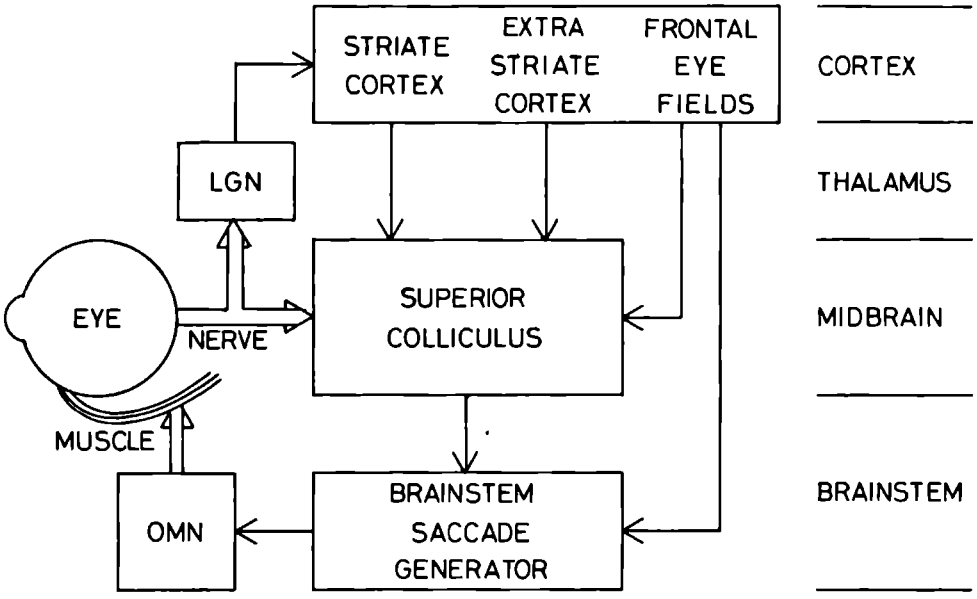

Figure 1. Anatomical scheme of the saccadic system. The frontal eye fields receive visual information via the lateral genicolate nucleus (LGN), the striate cortex, and the extra-striate cortex, successively. Several cortical areas including the frontal eye fields project tothe superior colliculus, which gets a direct retinal projection as well. The brainstem saccade generator receives a projection from the colliculus and an independent input from the frontal eye fields. The oculomotor nuclei (OMN) obtain their saccade command signal from the brainstem saccade generator. This model is oversimplified: many additional structures should be included, and the areas shown could be elaborated. (after: Bruce and Goldberg, 1984)

the receptive field location, if no stimulus was presented there. Unlike visual cells, QV cells may show a prolonged activity to a very brief stimulus presentation. Furthermore, they do not show the ordinary saccade-related burst as in movement cells: neither discharge onset nor peak frequency are tightly linked to the moment of saccade initiation. The QV cells are thought to code motor error, also if the error arises from a combination of the remembered target position and the vector of an eye movement made after the extinction of that target (Mays and Sparks, 1980).

Since after the ablation of the SC saccades can still be made, this structure does not seem exclusively responsible for the generation of saccades in the monkey.If however,the frontal eye fields (FFF) are also ablated the ability to produce saccades is permanently lost. This suggests the existence of two or more parallel pathways in the central part of the saccadic system (See scheme of the saccadic system in Figure 1).

It is surprising that the function of the SC in the generation of saccades has never been modeled quantitatively. This is in remarkable contrast with the existence of several quantitative models on the motor part of the saccadic system (see above). In chapter III a first step has been taken towards a model description of the spatial features of the neural processes in the superior colliculus. The application of this model is illustrated on the visuo-motor cell data (chapter III).

All electrophysiological recordings in the SC, so far reported in the literature, were made during the execution of a simple saccadic detection task. As a consequence, the relation between the burst rate in movement-related cells and the metrics of the ensuing saccade has only been established under that condition. Whether the colliculus is involved similarly in the generation of saccades during a task, in which a discrimination based on a colour cue is required, has been investigated in this thesis, for the first time, by the application of stimuli consisting of the simultaneous presentation of a green target and a red

nontarget (chapter IV).

To be able to predict the behaviour of the monkey's saccadic system in response to target/nontarget stimuli the electrophysiological experiments were preceded by extensive behavioural experiments in humans with double-spot stimuli. In the first series of these experiments the saccadic response to double-target stimuli during a simple saccadic detection task was investigated. The results describe the distribution of saccadic endpoints, which appears to depend upon the relative position of the targets. The double spot positions were varied systematically either in direction or in eccentricity (chapter I).

In a second series of double-spot experiments with human subjects we applied the target/nontarget stimuli, which were later used in the electrophysiological studies with monkeys. The experimental paradigm was designed to discover whether an increase in the percentage of correct responses in the discrimination task would be related to an extra delay in saccade initiation.

References

Bruce C.J. and Goldberg M.E. (1984) Physiology of the frontal eye fields. TINS November 1984, 436-441.

Fuchs A.F., Kaneko C.R.S. and Scudder C.A. (1985) Brainstem control of saccadic eye movements. Ann. Rev. Neurosci. 8, 307-337.

Mays L.E. and Sparks D.L. (1980) Dissociation of visual and saccade-related responses in superior colliculus neurons. J. Neurophysiol. 43, 207-232.

Robinson D.A. (1981) The use of control systems analysis in the neurophysiology of eye movements. Ann. Rev. Neurosci. 4, 463-503.

Schiller P.H. (1984) The superior colliculus and visual function. In Handbook of Physiology Section 1, Volume III, pp. 457-505.

Sparks D.L. and Pollack J.G. (1976) The neural control of saccadic eye movements: the role of the superior colliculus. In Eye Movements (Edited by Brooks B.A. and Bajandas F.J.) Plenum Press New York. pp. 179-219.

Wurtz R.H. and Albano J.E. (1980) Visual-motor function of the primate superior colliculus. Ann. Rev. Neurosci. 3, 189-226.

Wurtz R.H., Goldberg M.E. and Robinson D.L. (1980) Behavioral modulation of visual responses in the monkey: stimulus selection for attention and movement. Progress in Psychobiology and Physiological Psychology 9, 43-83.

METRICS OF SACCADE RESPONSES TO VISUAL DOUBLE STIMULI: TWO DIFFERENT MODES

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Abstract—Earlier studies using visual double stimuli along the horizontal axis have revealed a strong *averaging* tendency in the saccadic system This study shows averaging also for equally eccentric double stimuli with a modest difference in *direction* ($\Delta\phi = 30$ deg) When the difference is enlarged ($\Delta\phi = 90$ deg) the response pattern becomes *bistable* i e the eye jumps near either one or the other stimulus This bistable response mode is reflected also in saccade *amplitude* when double stimuli along the horizontal axis have a large difference in eccentricity It is concluded that the saccadic system response mode to double stimuli depends on interstimulus spacing Furthermore, both types of response can be shown to exist with double stimuli confined to one visual half-field

Saccade metrics Visual system Target selection Double-step responses Double-spot responses Human

INTRODUCTION

Recently, several studies using visual double stimuli have shown that when two retinal locations at different eccentricities but at the same meridional angle are stimulated sequentially (Becker and Jurgens, 1979, Van Gisbergen *et al*, 1981) or simultaneously (Coren and Hoenig, 1972, Findlay, 1982) the resulting saccade is often directed at a position between the two targets This phenomenon has been denoted as "*averaging*" or as global effect The averaging effect is not evident when two simultaneously presented stimuli are in two different half-fields, i e on opposite sides of the fixation point (Findlay, 1980, Levy-Schoen, 1969) In this case the saccadic system shows a *bistable* response it selects either one or the other stimulus

Electrophysiological studies on visuomotor cells which are assumed to be involved in the generation of visually guided saccades (Wurtz and Mohler, 1976, Goldberg and Bushnell, 1981) have also used single and double stimuli Analysis of responses to double-spot stimuli has led to the determination of the spatial selectivity of the so-called enhancement phenomenon It has been suggested by Wurtz and Albano (1980) that this neural mechanism might play a role in target selection for the saccadic system

These findings have led us to do further behavioural studies employing a wider variety of double stimuli More specifically, we wanted to investigate if the bistable response mode can also be demonstrated for double stimuli presented along the horizontal meridian in *one half-field* Earlier studies found bistable responses only when both stimuli were in different half-fields and indicated that double stimuli presented in one half-field lead to averaging responses We wondered, however, whether the saccadic response might become bistable also in the case of a one half-field double stimulus when the spatial separation between the two alternative targets was made sufficiently large

To investigate this, both sequentially and simultaneously presented double stimuli were used It appeared that both response modes of the saccadic system (averaging, bistability) can be elicited with either type of one half-field stimulus The critical variable determining which mode will occur seems to be stimulus distance

The next question we asked, was whether the averaging response mode is linked exclusively to mechanisms determining saccade amplitude This possibility should be considered as, until now, averaging has been reported only with double stimuli having an eccentricity difference Therefore, in a second series of experiments, simultaneous double stimuli—again in one half-field—were given a difference in *direction* but were at the same eccentricity Both response modes could clearly be demonstrated also in these experiments and again interstimulus distance seemed to be the determining variable

Possible interpretations of these findings in relation with the results of electrophysiological experiments will be discussed

I. DOUBLE-STEP EXPERIMENTS

Methods

Three dark-adapted subjects (J G , H C and K S), with their heads fixated, were instructed to track a spot of light as quickly and as accurately as possible

The spot, which had a diameter of 0.5 deg and a luminance of 4.5 cd/m^2, moved horizontally on a dark screen placed at a distance of 57 cm.

Stimulus

The stimulus consisted of a series of single and double steps in random order. The double-step trials are identified by the amplitudes of first and second steps. For example: the (+15/+45) double step consists of a first step of 15 deg and a second step of 45 deg both in the same direction, thus moving the target ultimately 60 deg from the original fixation point. Each stimulus sequence contained 6 single steps (15, 30 and 45 deg; each presented twice) and 20 double steps. The double steps had five different amplitude combinations (+15/+15, +15/+45, +15/−30, +30/−15, +45/+15 deg), each of which was applied with four different interstep times (50, 100, 150 or 200 msec). Initial direction and initial fixation position as well as the temporal order were randomized. Inter-trial pauses varied randomly from 2 to 6 sec. Each stimulus type was presented at least 45 times to each subject in a period of one month

Eye-movement recording

Horizontal eye movements were recorded with the d.c.-coupled EOG-technique Saccade amplitude could be measured with an accuracy of 1 deg or better. The low-pass filtered (−3 dB at 50 Hz) eye position signal was digitised with a resolution of 12 bits at a rate of 500 samples/sec and stored in computer files for analysis. Saccade detection was

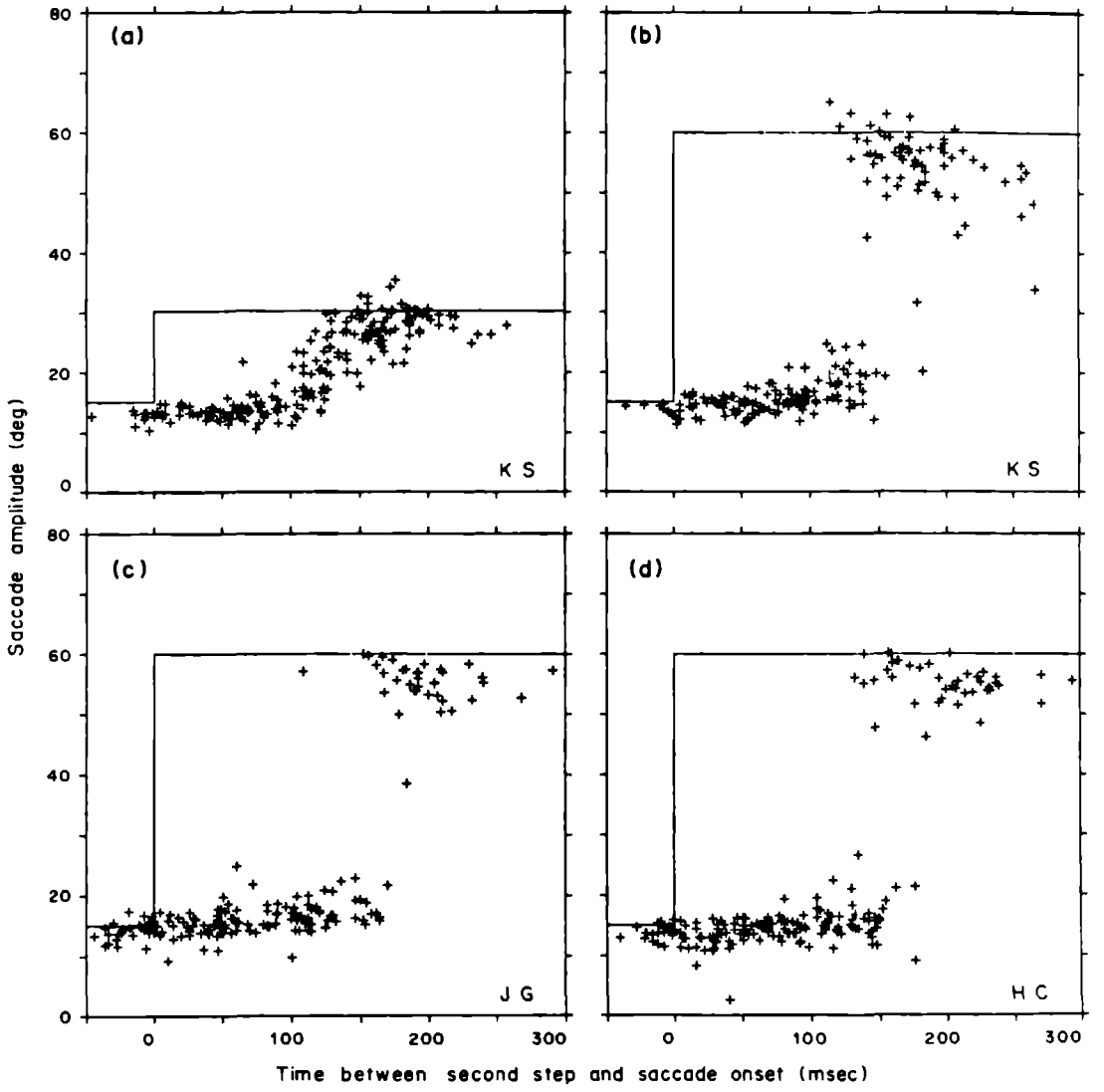

Fig. 1. Plot of first-saccade amplitudes vs the delay between the second step and saccade onset in double-step trials. Saccades obtained in trials with various interstep times (see Methods) were pooled. First-step size was 15 deg in all experiments shown. Second-step size is indicated in each panel (a) second-step size 15 deg; subject K.S. (b), (c) and (d) Second-step size 45 deg; subjects K.S., J.G. and H.C. respectively.

performed by a computer program using a velocity-threshold criterion and was checked subsequently by visual inspection of the eye movement record together with the detected onset and offset moments Responses were pooled over stimulus direction

Some results of these experiments have been reported in a preliminary form elsewhere (Van Gisbergen *et al*, 1981) In this paper we only consider the first saccade responses

Results

Figure 1 shows the amplitude of first saccadic responses to double-step stimuli as a function of the delay (Becker and Jurgens, 1979) between second target step and saccade onset This delay can be negative for interstep times of 150 msec or longer Panel (a) of Fig 1 contains the data obtained from subject K S with a second step size of 15 deg, whereas panels (b), (c) and (d) show responses for a second step size of 45 deg for all three subjects The responses to the four different interstep times (50, 100, 150 and 200 msec) have been pooled The amplitudes of saccades starting less than 100 msec after the second step still correspond to the initial target position Responses with a delay or more than 200 msec have amplitudes related to the final target position

When the amplitude of the second step (ΔE) was 15 deg, the transition from initial to final target position occurred gradually with many intermediate saccades scattered along a *smooth contiguous curve* [Fig 1(a)], as has also been described by Becker and Jurgens (1979) The amplitude histogram of first saccades with delays between 100 and 200 msec made in response to $\Delta E = 15$ deg double steps is unimodal [Fig 2(a)], due to the large number of saccades with intermediate sizes

In contrast, *a clear gap* in the saccade size distribution occurred for all three subjects when ΔE was 45 deg [Fig 1(b), (c), (d)] The histograms [Fig 2(b), (c), (d)] demonstrate that, within the mentioned range of delays, amplitudes related to both the first and the final target position occur while intermediate amplitudes are virtually absent These bimodal distributions for large step sizes cannot be accounted for by an absence of saccades in a certain delay range, since there is no gap in the delay distribution

II DOUBLE-SPOT EXPERIMENTS

Methods

Two subjects (J G and F O) were instructed as in the double-step experiments The visual target was a green (Kodak Wratten filter No 58) spot of light with a diameter of 0 4 deg (for adjustments of target diameter in double spot experiments see paragraph on "bias" in this section) and a luminance of 5 cd/m^2, which was rear projected on a translucent screen This screen was placed at a distance of 57 cm and had a white background illumination of 1 2 cd/m^2

Stimuli

In all stimulus sequences, each of the 80 trials started with the presentation of a fixation spot After a random period (varying from 500 to 1100 msec) this central spot was switched off and the screen was empty for 12 msec In the great majority of trials (72/80) this gap was followed by the appearance of a target somewhere in the periphery During double-stimulus trials (8/80), two spots were presented simultaneously The positions of the two spots were not varied within one sequence of 80 trials We used four different double-spot configurations in eccentricity experiments both spots were on the righthand horizontal axis and had a difference in eccentricity (ΔE) of 10 or 30 deg, in direction experiments the spot positions had the same eccentricity (20 deg) and a difference in direction ($\Delta\phi$) of either 30 or 90 deg Subjects were instructed to track the target as quickly and as accurately as possible No additional instruction pertaining to the double-spot trials was given To discourage a preconceived response strategy, only 10% of the trials consisted of double spots

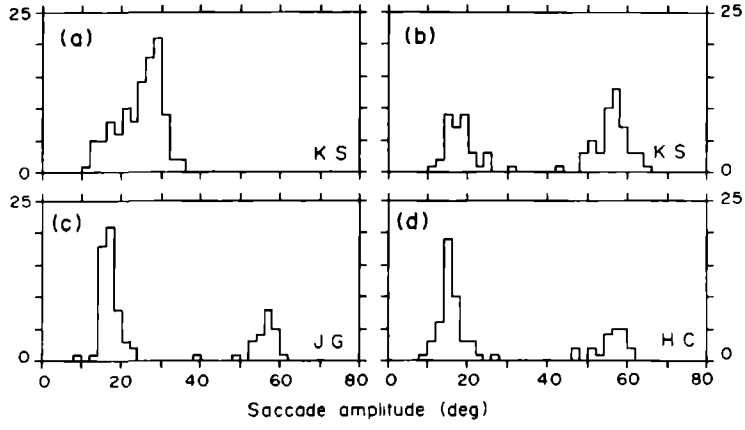

Fig 2 Amplitude histograms of first saccade responses with a delay between 100 and 200 msec (see also Fig 1) In panel (a) the second stimulus step was small (15 deg), in the other panels data from all three subjects in response to the stimulus with a large second step (45 deg) are shown

For the same reason the two target presentation, which is potentially confusing, had a short duration after 250 msec (sufficiently long to elicit the first saccade) at random either one or the other target was switched off In the Discussion we list several reasons why we think that the responses to these double stimuli were not influenced by a preconceived strategy anymore than the single spot responses In eight trials, a single target was presented at one of the double-spot positions, these served as a control for the double-stimulus trials In the remaining 64 single target trials the peripheral spot was positioned at random eccentricity and direction unrelated to the double spot positions Different versions of these stimulus sequences were presented up to five times to each subject and for each of the four stimulus configurations

Eye movement recording

The movements of the left eye were recorded with the double magnetic induction method (Reulen and Bakker, 1982) An improved version of this method developed in our group (Bour *et al*, 1984), permits a measuring range of about 30 deg in all directions and has an angular resolution of 7 or better up to 25 deg eccentricity The static nonlinearity inherent in this method was corrected using a computerised two-dimensional mapping procedure The data base for

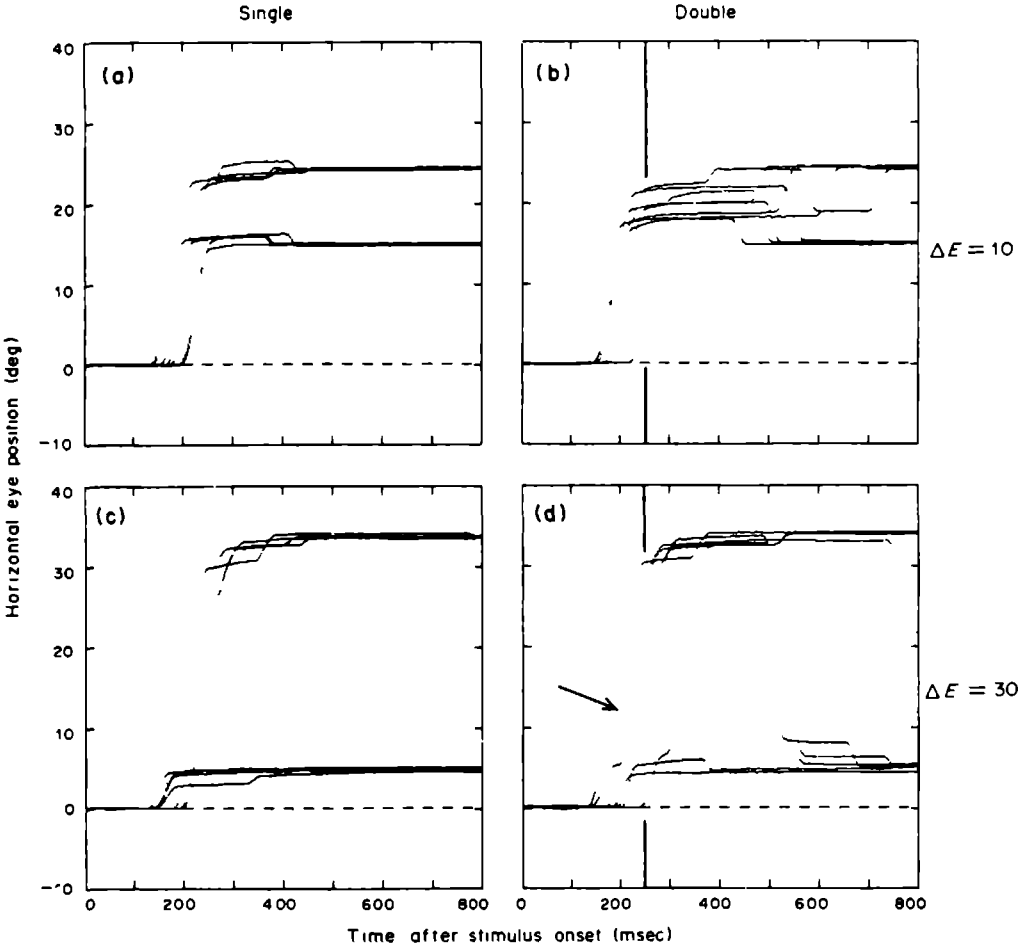

Fig 3 Horizontal eye movements of subject F O recorded after the presentation of single spots [(a) and (c)] and of double spots [(b) and (d)] during ΔE double-spot experiments Each panel contains eight superimposed responses The scaling along the vertical axis is relative to eye position during stimulus onset In the range of 30–35 deg the eye position is slightly off scale, caused by an imperfect correction of the nonlinearity in the eye movement recording (see Methods) In panels (a) and (b) (ΔE = 10 deg experiments) the subject had a small bias which was left uncorrected *panel* (*a*) the target was at 15 or 25 deg eccentricity, the spot diameter was 0 4 deg for both near and peripheral target, *panel* (*b*) both targets from panel (a) were presented simultaneously In panels (c) and (d) (ΔE = 30 deg experiments) the subject had a large bias To obtain yet a balanced set of double spot responses the peripheral target diameter was enlarged to 1 3 deg *panel* (*c*) responses to single spot stimuli with either a small spot at 5 deg eccentricity or a large spot at 35 deg In *panel* (*d*) these targets were presented simultaneously In panel (d) the arrow indicates an example of a composite saccade (see text) In the double-spot panels [(b) and (d)] a vertical interrupted line indicates the time when one of the two spots is turned off

this correction procedure consisted of sets of raw eye-position signals measured at 73 stimulus positions The low-pass filtered (−3 dB at 150 Hz) signals were digitised with a precision of 12 bits at a rate of 500 samples/sec in each channel and stored in computer files for analysis

In $\Delta\phi$ experiments, with the targets at an eccentricity of 20 deg, the central fixation position coincided with the center of the measuring range at the primary position In ΔE experiments with target positions of up to 35 deg to the right, some eye movements would fall beyond the measuring range To prevent this, the central fixation point was shifted 10 deg to the left from the primary position After linearization correction, the relation between stimulus position and corrected eye position did not deviate by more than 0 4 deg from linearity, except in the $\Delta E = 30$ deg experiments where a remnant of the saturation in the range of 30–35 deg remained after correction This mild (3%) discrepancy from linearity does not in any way endanger our conclusions

Response bias

In double-spot experiments, with two targets presented on the horizontal axis at different eccentricities, it has been reported that most of the saccades are directed at the nearest spot position This phenomenon, called bias, is little understood so far (Findlay, 1980) A response with saccades more likely directed at the far target can be obtained by either increasing the size of the far target (Findlay, 1980) or by delaying the onset moment of the near target (Levy-Schoen, 1969)

In our double-spot experiments, it appeared in conformity with the authors cited above, that the saccadic system may show a spatial bias towards one of the target locations For example, we found in $\Delta E = 30$ deg experiments that virtually all saccades of both subjects were directed at the near target with an eccentricity of 5 deg, and were almost totally ignoring the physically identical target at 35 deg With such an extremely asymmetrical distribution of endpoints it is impossible to decide whether the response is averaging or bistable (see Introduction) A response consisting of saccades near one target only could have originated from an "averaging" unimodal endpoint distribution which shifted towards the preferred target, but equally well from a "bistable" bimodal distribution of which the mode near the non-preferred target remained empty In order to distinguish between endpoint patterns that stay unimodal and those which become bimodal, when bias is compensated, we studied only symmetrical distributions, which could always be obtained by adjusting the target diameters

In our double-spot experiments the idiosyncratic bias, if present, was countered for each subject and each configuration as stated below In response to the $\Delta E = 10$ deg stimuli, with identical spots at 15 and 25

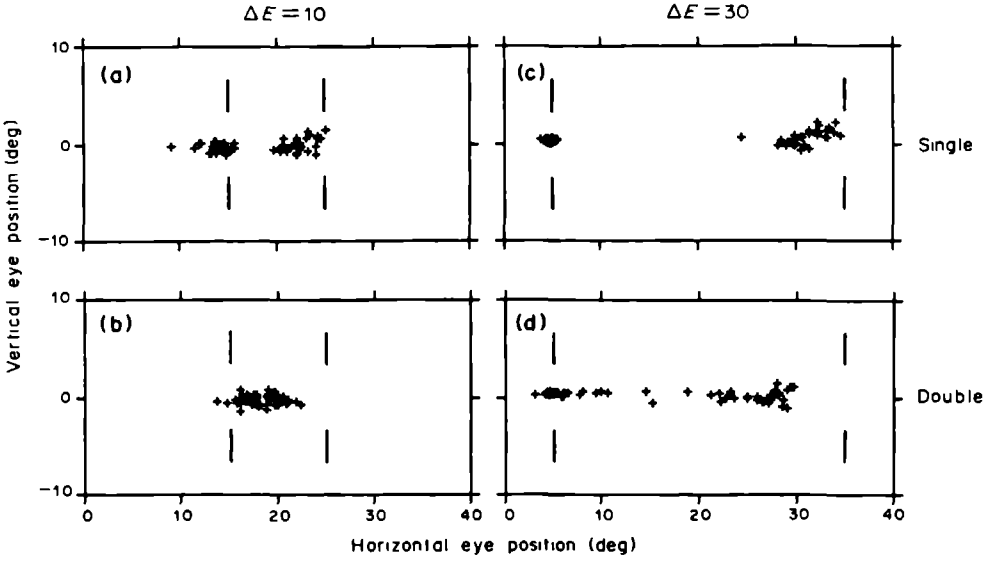

Fig 4 Position plots of endpoints of first saccades made in response to single-spot [(a) and (c)] and ΔE double-spot stimuli [(b) and (d)] by subject J G To enable comparison of saccade endpoints in single-spot and double-spot trials, the panel configuration is changed relative to Fig 3 Stimulus position is indicated with the center of the interrupted vertical line segment The central fixation position coincides with the middle of the left edge of each panel (a) Responses to single spot targets with a 0 4 deg diameter along the horizontal axis with an eccentricity of 15 or 25 deg (b) Metrics of responses when the stimuli in panel (a) were presented simultaneously saccades with intermediate amplitudes prevail (c) Single-spot stimulus responses to a target at 5 deg eccentricity with a diameter of 0 3 deg or a target at 35 deg eccentricity with a diameter of 2 0 deg (d) Metrics of responses when both stimuli of (c) were presented simultaneously Nearly all saccades are directed at either the nearest or the most peripheral target

Table 1. Latencies of saccades made in response to double-spot and single-spot control stimuli Mean values and standard deviations in milliseconds. N is number of saccades in each sample

	Subject J G						Subject F O					
	Single		Double				Single		Double			
Stimulus	Mean	SD	Mean	SD	S	N	Mean	SD	Mean	SD	S	N
$\Delta E = 10$	168	18	166	19	*	56	167	19	163	26	*	40
$\Delta E = 30$	172	19	183	25	*	62	162	25	164	28	*	40
$\Delta\phi = 30$	168	16	164	14	*	43	185	37	172	29	*	16
$\Delta\phi = 90$	168	18	193	30	**	55	193	17	231	22	**	38

The significance (S) of the difference between the latency distribution of double-spot and single-spot responses was determined by a two-sided Wilcoxon-test *Not significant, $P > 0.05$ and **highly significant, $P < 0.005$)

deg eccentricity, both subjects had only a trifling bias toward the nearest spot [Figs 3(a), (b) and 4(a), (b)]. Spot diameters remained 0.4 deg. In stimuli with spots at an eccentricity of 5 and 35 deg ($\Delta E = 30$ deg) the spot size of the peripheral target had to be greatly enlarged [Figs 3(c), (d) and 4(c), (d)]. For subject F.O. a balanced response was obtained with near and more-peripheral target diameters of 0.4 and 1.3 deg, respectively. In subject J.G. these values were 0.3 and 2.0 deg. With both $\Delta\phi$-stimuli subject J.G. had a slightly downward bias for physically identical spots (Figs 6, 7). Here in subject F.O. the bias was larger and in opposite direction. His direction histogram of first saccades $\Delta\phi = 30$ deg stimuli again showed averaging, but was skewed towards the upper target. To achieve a balanced response in the $\Delta\phi = 90$ deg experiments the diameter of the lower target had to be doubled (to 0.8 deg) for this subject.

In order to compare double-spot responses with single-spot responses the diameter of the single-spot control stimulus equaled that of the target in the double-spot stimulus at the same location.

Results

(*a*) *ΔE double-spot stimuli.* In these experiments two spots were presented simultaneously along the right horizontal axis at different eccentricities. Responses of subject F.O. to these ΔE double spots, all obtained in a single experiment, are shown superimposed in Fig. 3(b), (d). The large saccades after 400 msec in the double spot trials are made towards the remaining stimulus after one of the pair was switched off. The corresponding single spot responses, used as a control, are shown in Fig. 3(a), (c).

From examining the amplitudes of first saccades made to double-spots, it appears that the shape of their distribution depends upon the size of the inter-stimulus eccentricity difference.

During experiments with a small difference in eccentricity ($\Delta E = 10$ deg) most first saccades to the double-spot stimulus [Fig. 3(b)] have amplitudes which are intermediate between those of saccades made in response to the single spot control stimuli [Fig. 3(a)]. This is demonstrated more thoroughly in the plots of endpoints of all first saccades of subject J.G. in response to the same stimuli [Fig. 4(a), (b)]. To construct each plot, data obtained from at least 6 experiments (48 or more stimuli) were pooled. Nearly all double-spot saccades ended on a position in between the two spots [Fig. 4(b)]. The amplitudes of these *averaging* responses are represented in a histogram, which appears to be unimodal [Fig. 5(b)]. Latencies, defined as the time between peripheral target onset and the initiation of the first saccade, of the responses in this experiment were compared. The double spot responses have latencies which fall in the same range as those of first saccades to single-spot stimuli (Table 1).

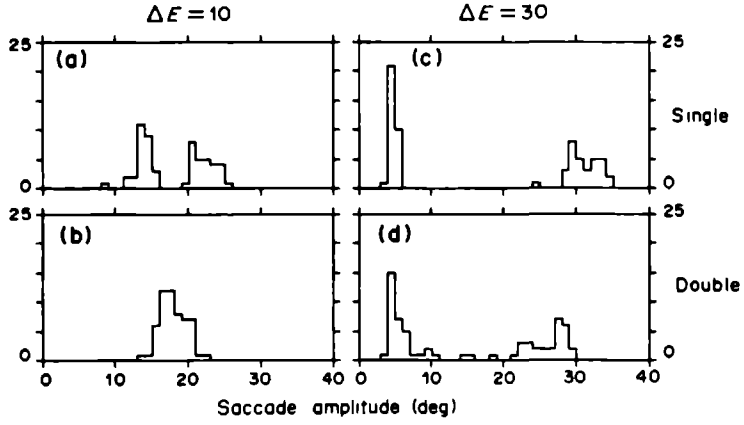

Fig. 5. Amplitude histograms of first saccades. Data from 56 responses to single- and double-spot $\Delta E = 10$ stimuli, and from 62 saccades for both $\Delta E = 30$ stimulus types. Computed from the data in Fig. 4 (same panel composition), bin width. 1 deg.

A clearly different result, as far as the size distribution of first saccades is concerned, was obtained in experiments with a large separation in eccentricity between the targets ($\Delta E = 30$ deg) These double stimuli elicit first saccades which are either rather small (directed to the nearest target) or very large (ending near the more peripheral spot), but rarely of intermediate size This can be seen in the typical examples of eye-movement responses [Fig 3(d), subject F O] as well as in the endpoint plots of all first saccadic responses [Fig 4(d), J G] We call this response pattern *bistable* The amplitude histogram [Fig 5(d)], representing the data of all first saccades in 64 double-spot trials, is clearly bimodal Again, no significant difference between the latency distributions of double and single spot responses exists (Table 1)

A peculiarity noticed in the single spot controls of the $\Delta E = 10$ deg experiment was that first saccades of subject F O sometimes showed static overshoot [Fig 3(a)] This phenomenon, however, was rare in the second subject [see Fig 5(a)] The occurrence of these hypermetric saccades is unexplained, but may be related to the eccentrical fixation position before the saccade was made (see Methods)

In the $\Delta E = 30$ deg double spot condition, a second saccade may start after a very short intersaccadic interval [Fig 3(d), see also Becker and Jurgens, 1979] In subject F O , where this phenomenon is most clear, about 10% of the double-spot responses ($\Delta E = 30$ deg) were *composite saccades* These eye movements seem to consist of a small initial saccade and a second rapid movement which modifies the first saccade in midflight We interpreted these movements as a single large saccade Our conclusions would still be justified if one would interpret these movements as an initial small saccade followed, with a zero interval, by a second corrective saccade

In double-spot trials, [Fig 3(b), (d)] randomly one of the two spots is turned off after 250 msec At this moment all first saccades have started, but some are not yet finished It has been reported (Becker and Jurgens, 1979) that saccades are not visually influenced less than about 100 msec before saccade offset Since all first saccades end within 100 msec

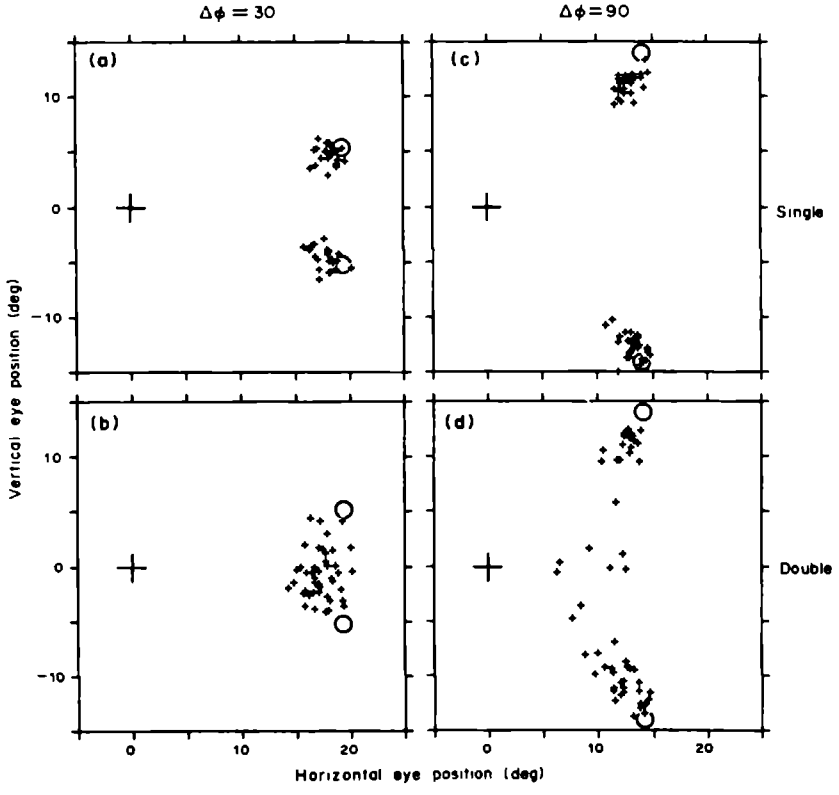

Fig 6 Metrics of first saccades made in response to single-spot (upper part) and $\Delta\phi$ double-spot stimuli (lower part of figure) by subject J G Stimulus positions are indicated by circles (size not exactly to scale), fixation position is denoted by a large cross on the left of each panel (a) Single-spot stimulus responses to targets with a direction of either +15 or −15 deg relative to the positive horizontal axis (b) Metrics of first-saccades made when the stimuli of panel (a) were presented simultaneously Intermediate saccades prevail in this condition (c) single spot stimulus responses to targets with equal diameters of 0 4 deg and directions of either +45 or −45 deg relative to the positive horizontal axis (d) Metrics of first saccades when both stimuli in panel (c) were presented simultaneously Most saccades are directed near the upper or near the lower stimulus

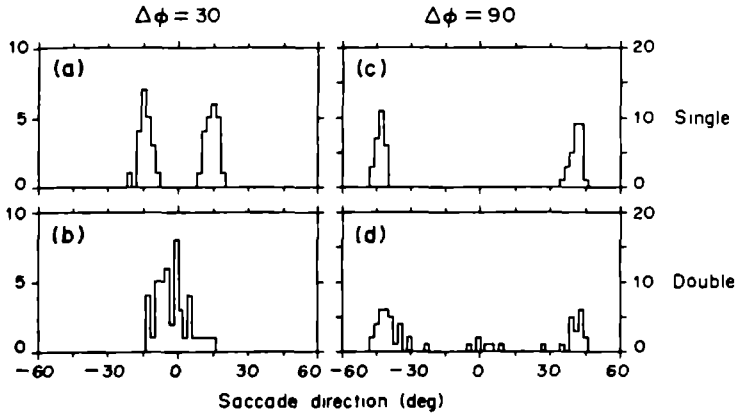

Fig 7 Direction histograms of first saccades Computed from data in corresponding panels of Fig 6 by using M = arctan (tan θ_V/tan θ_H), where M is saccade direction, θ_H is horizontal saccade amplitude and θ_V is vertical saccade amplitude Note difference in scaling of vertical axes Bin width 2 deg

after one target is switched off, we think they are not affected by this stimulus change

(*B*) *Δφ double-spot stimuli* In this version of the double-spot experiment both targets were placed at the same eccentricity (20 deg) and in different directions Endpoints of first saccades to these Δφ double-spots are shown in Fig 6 The metrics of saccades to these double-spot stimuli is related to the size of the direction difference (Δφ)

For small values of this inter-target parameter (Δφ = 30), the results show *averaging* responses, i e all first saccades are directed in between the two targets [Fig 6(b)] Each first saccade is followed by one or more corrective saccades toward the remaining target The direction histogram of first saccades in the Δφ = 30 condition is unimodal [Fig 7(b)] The mean latency of these averaging saccades does not differ from that in corresponding single-target trials (Table 1)

When the inter-target difference in direction is enlarged (Δφ = 90) the response pattern becomes *bistable* for both subjects This can be seen from the direction histogram of all 55 double-spot trials of subject J G , which is clearly bimodal [Fig 7(d)] However some responses still have an endpoint somewhere in between both targets [Fig 6(d)] The distribution of latencies of first saccades in these trials is significantly different from that in comparable single spot trials (Table 1) Thus, double-spot latencies are prolonged for large separations in direction

DISCUSSION

Experimental paradigm

Before comparing our results with the literature it is first discussed why we think the results do not depend critically upon the experimental paradigm used In all experiments subjects were instructed to track the target as accurately and as quickly as possible They were not explicitly told what to do in response to the randomly, rarely and shortly presented double-spot stimuli The question arises would the measured averaging responses be absent if the instruction had been to selectively track one of the two stimuli? Several lines of evidence indicate that this is not the case

Firstly, when double-spot trials consisted, instead of two green spots, of a red-green pair and subjects were instructed to track the green spot while ignoring the rarely occurring red spot, the averaging responses persisted *Secondly*, all single-spot latencies in our experiments are in accordance with those in other saccade studies with single spot stimuli (Findlay, 1983) The lack of a clear latency increase for the averaging double-spot responses relative to single-spot responses indicates that both are governed by the same neural processes In other words, it is unlikely that averaging in double-spot responses should result from an additional instruction-dependent process, yet without increasing the saccade latency And *thirdly*, in a discrimination experiment, in which the difference between two—peripherally and simultaneously presented targets could only be perceived with high acuity vision (i e precise foveal fixation), Findlay (1982) found that first saccades also showed averaging These data suggest, that first saccades, which are not accurately directed at the target, cannot be avoided In Findlay's comparison task, saccades may point in between both targets, instead of bringing the eye on target at once Also in our target/non-target experiments with 10–15% double-spot stimuli, the response was bistable, or unimodal, depending on Δφ, and thus 50%, or 100%, of the saccades were not accurately directed at the target

Two experiments recently conducted in our laboratory, however, show that in certain target/non-target tasks with specific instruction all first saccades can be made in the direction of the target, ignoring the disturbing spot, which was presented at the same eccentricity of 20 deg, but had a small difference in direction First, if the subject knows the target posi-

tion in advance as in a train of identical trials with a green target and a red non-target spot always presented at the same positions, the saccade direction shifts from midway between both spots in the first trial, to that of the target in following trials Second, in target non-target experiments with as many as 70% double-spot trials, nearly all first saccades (90% or more) were pointed at the target, but only if subjects got an explicit instruction to avoid fixation of the red spot and received feedback about their performance Many of these saccades had latencies, which were longer than those observed in the 10% target non-target experiments A clear speed-accuracy trade-off was observed responses with latencies below about 300 msec still showed averaging but all saccades with longer latencies were correctly directed at the target

Response metrics two different modes

Our main new finding is that the response of the saccadic system to double stimuli depends on inter-target distance If the targets are close together an *averaging* response is made, which directs the gaze in between both targets This has been reported earlier for the amplitude of the responses to sequentially presented targets (Becker and Jurgens, 1979, Van Gisbergen *et al*, 1981) as well as for simultaneously presented targets (Coren and Hoenig, 1972, Findlay, 1982), all presented along the horizontal axis We present evidence here, that it also exists for differences in direction

For a large interspot distance the response is most often directed to one or the other target Results in this paper show for the first time a *bistable* response to double-step stimuli with a large difference in eccentricity When targets are presented simultaneously, this response is also found for a sufficiently large difference either in direction or in eccentricity We regard this as an important result since it demonstrates that bistability, shown earlier with double stimuli on opposite sides of the fixation point (Levy-Schoen, 1969, Findlay, 1980), can also be demonstrated in *one half-field*

The response categories "averaging" and "bistable" are probably extremes in a continuum, with a gradual transition from one response type to the other A few "averaging" saccades occur in responses with predominantly bimodal endpoint distributions [$\Delta E = 30$ deg experiments, Fig 5(d), $\Delta\phi = 90$ deg experiments, Fig 7(d)] In distributions which are clearly unimodal, a small number of saccades are directed purely at one of the targets [$\Delta E = 10$ deg experiments, Fig 5(b), $\Delta\phi = 30$ deg experiments, Fig 7(b)]

Could the observed mode depend upon bias compensation?

One may wonder whether it is possible to obtain any shape of endpoint distribution one would like to see, merely by adjusting the target sizes Several observations lead us to think that this is not the case When stimulus separation was relatively small, we always saw a unimodal response pattern This feature of the response pattern was not critically dependent on bias adjustment In cases where the bias compensation was insufficient, or overdone, the response histogram was skewed towards one or the other stimulus but *remained unimodal* under all circumstances The need to compensate for bias, in order to get meaningful reproducable results, which can be compared across subjects, is more obvious when stimulus separation is larger We have encountered conditions where double stimuli, with physically identical spots, yielded a clearly unimodal, but biased, response If bias was compensated this response pattern became symmetrical and distinctly bimodal For example, the response to $\Delta E = 30$ deg double stimuli was skewed towards the near stimulus and unimodal, when both stimuli were physically equal, but it was clearly bimodal, if bias was corrected In contrast, it was never possible to mold an asymmetrical bimodal distribution into a symmetrical unimodal pattern by compensating for bias We conclude that the potential range of the response patterns of the saccadic system depends on stimulus spacing For a given double stimulus configuration the extent of variation in response pattern is fixed Where in this range the system behaves is subject to individual differences (bias) and can be influenced by manipulating the physical features of the spots The effect of such manipulations, however, is limited under our conditions a small stimulus spacing never gave rise to a symmetrical bistable response and a large interstimulus distance could never elicit a symmetrical unimodal response

Comparison with electrical stimulation in superior colliculus

Indications that compromising responses to double stimuli are a typical property of the saccadic system can also be deduced from electrical stimulation studies Robinson (1972) found that, when stimulation at locus *A* in the superior colliculus in a monkey gave rise to a saccadic vector **A** and stimulation at locus *B* caused a vector **B**, stimulating both sites simultaneously elicited a saccade, which was a compromise between **A** and **B** The metrics of this saccade depended on the relative stimulation current strengths Similar results have been obtained in the frontal eye fields (Robinson and Fuchs, 1969) These electrical stimulation results have obvious similarities with some of our visual double-stimuli results [Figs 4(b) and 6(b)] It should be noted, however, that the electrical stimulation experiments did not yield bistable responses, even when **A** and **B** had appreciably different directions Quite recently it has been shown in the monkey that compromising saccades can also be elicited by combining a peripheral

visual target and an adequately timed electrical stimulus in the superior colliculus or in the frontal eye fields (Schiller and Sandell, 1983, Sparks and Mays, 1983)

Averaging a result of neural spatial filtering?

Electrophysiological studies have revealed that receptive and movement fields of neurons in the frontal eye fields (Goldberg and Bushnell, 1981) and the superior colliculus (Goldberg and Wurtz, 1972, Sparks *et al*, 1976) are often quite large The question arises whether the low spatial resolution capacity demonstrated in our experiments and those of Findlay (1982) may reflect *the coarseness of the neural maps* in these visuomotor areas To explain our data in such a scheme, one would have to assume that the two stimuli in the $\Delta\phi = 30$ deg experiments evoked a single large area of neural activity in these maps quite similar to the activity caused by one large visual stimulus centered between the two small spots (cf Findlay, 1982) When stimulus separation is sufficiently large, even the coarse neural map will reveal both alternatives to the motor system and necessitate a target-selection procedure which causes the response to become bistable Whatever the precise mechanism determining saccade metrics, we think it is likely to be based on a coarse two-dimensional neural map McIlwain (1976, 1982) has specified how neural activity in such a map might determine saccade amplitude and direction His scheme also bears on the problem how it is possible that the coarse neural representation of a visual target allows the saccadic response to single spots still to be rather precise [Figs 4(a), (c) and 6(a), (c)]

Distinct mechanisms for amplitude and direction?

The present study shows that the dependence of saccade direction upon the angular separation between the $\Delta\phi$ double-spot is similar to the relation between saccade amplitude and eccentricity difference of a ΔE double stimulus This does not support the idea, presented in the literature (e g Komoda *et al*, 1973), that the metrics computation involves distinct and sequentially ordered subsystems responsible for the generation of saccade direction and saccade amplitude On the contrary, it suggests that amplitude and direction of the saccade endpoint are generated in a very similar way Electrophysiological studies have revealed that early stages of stimulus processing which ultimately lead to the execution of a saccade, take place in retinotopic representations of the stimulus scene Determination of the saccade endpoint by uniform spatial processing within such neural maps could explain our data

Latency

As stated above, latencies in $\Delta\phi$ and ΔE double spot experiments with small interstimulus distances, yielding averaging responses, were not significantly different from corresponding single-spot trials For large stimulus separations, which led to a bistable response, double-spot latency was clearly prolonged in $\Delta\phi$, but not in ΔE experiments (Table 1) These double-spot results are in accordance with certain latency effects in double-step experiments It has been reported that the first saccade latency distribution observed in response to stimuli with a small second step was about the same as the results obtained with single steps (Becker and Jurgens, 1979) When the second step brought about a large change in stimulus direction ($\Delta\phi = 180$), the latency distribution became bimodal Saccades in the early mode went to the first target and all late saccades, after the gap, went to the final target (Wheeless *et al*, 1966, Becker and Jurgens, 1979, Hou and Fender, 1979) In our subjects saccades going to the final target had a significantly prolonged mean latency, relative to the second step, in $\Delta\phi = 180$ deg experiments, but this was not seen for double-steps with $\Delta E = 30$ deg (unpublished latency data)

Thus it seems that a large ΔE value may make the metrics system bistable, but does not delay the saccade initiation This is different from the $\Delta\phi$ domain, where metrics bistability and latency prolonging concur in the response

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REFERENCES

Becker W and Jurgens R (1979) An analysis of the saccadic system by means of double step stimuli *Vision Res* **19,** 967–983

Bour L J, Van Gisbergen J A M Bruijns J and Ottes F P (1984) The double magnetic induction method for measuring eye movement results in monkey and man *IEEE Trans Biomed Engng* **BME-31,** 419–427

Coren S and Hoenig P (1972) Effect of non-target stimuli upon length of voluntary saccades *Percept Mot Skills* **34,** 499–508

Findlay J M (1980) The visual stimulus for saccadic eye movements in human observers *Perception* **9,** 7–21

Findlay J M (1982) Global visual processing for saccadic eye movements *Vision Res* **22,** 1033–1045

Findlay J M (1983) Visual information processing for saccadic eye movements In *Spatially Oriented Behaviour* (Edited by Hein A and Jeannerod M) Springer Berlin

Goldberg M E and Wurtz R H (1972) Activity of superior colliculus in behaving monkey I Visual receptive fields of single neurons *J Neurophysiol* **35,** 542–559

Goldberg M E and Bushnell M C (1981) Behavioral enhancement of visual responses in monkey cerebral cortex II Modulation in frontal eye fields specifically related to saccades *J Neurophysiol* **46,** 773–787

Hou R L and Fender D H (1979) Processing of direction and magnitude by the saccadic eye-movement system *Vision Res* **19,** 1421–1426

Komoda M K, Festinger L, Phillips L J Duckman R H and Young R A (1973) Some observations concerning saccadic eye movements *Vision Res* **13,** 1009 1020

Levy-Schoen A (1969) Determination et latence de la reponse oculo-motrice a deux stimulus simultanes ou successifs selon leur excentricite relative *Ann Psychol* **69,** 373–392

McIlwain J T (1976) Large receptive fields and spatial transformations in the visual system In *International Review of Physiology, Vol 10, Neurophysiology II* (Edited by Porter R) Univ Park Press, London

McIlwain J T (1982) Lateral spread of neural excitation during microstimulation in intermediate gray layer of cat's superior colliculus *J Neurophysiol* **47,** 167–178

Reulen J P H and Bakker L (1982) The measurement of eye movement using double magnetic induction *IEEE Trans Biomed Engng* **BME-29,** 740–744

Robinson D A and Fuchs A F (1969) Eye movements evoked by stimulation of frontal eye fields *J Neurophysiol* **32,** 637–648

Robinson D A (1972) Eye movements evoked by collicular stimulation in alert monkey *Vision Res* **12,** 1795–1808

Schiller P H and Sandell J H (1983) Interactions between visually and electrically elicited saccades before and after superior colliculus and frontal eye field ablations in the rhesus monkey *Exp Brain Res* **49,** 381–392

Sparks D L , Holland R and Guthrie B L (1976) Size and distribution of movement fields in the monkey superior colliculus *Brain Res* **113,** 21–34

Sparks D L and Mays L E (1983) Spatial localization of saccade targets I Compensation for stimulation-induced perturbations in eye position *J Neurophysiol* **49,** 45–63

Van Gisbergen J , Gielen S , Cox H , Bruijns J and Kleine Schaars H (1981) Relation between metrics of saccades and stimulus trajectory in visual target tracking, implications for models of the saccadic system In *Progress in Oculomotor Research* (Edited by Fuchs A F and Becker W) Elsevier-North Holland, Amsterdam

Wheeless L Jr, Boynton R and Cohen G (1966) Eye-movement responses to step and pulse-step stimuli *J opt Soc Am* **56,** 956–960

Wurtz R H and Albano J E (1980) Visual-motor function of the primate superior colliculus *Ann Rev Neurosci* **3,** 189–226

Wurtz R H and Mohler C W (1976) Organization of monkey superior colliculus enhanced visual response of superficial layer cells *J Neurophysiol* **39,** 745–765

LATENCY DEPENDENCE OF COLOUR-BASED TARGET VS NONTARGET DISCRIMINATION BY THE SACCADIC SYSTEM

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Abstract—First saccade responses to sudden presentations of a target nontarget stimulus consisting of green and red spots of light have been investigated This paradigm which avoids certain ambiguities present in earlier experiments with identical double stimuli leads to remarkably similar conclusions We found again that the saccadic system had short-latency compromising responses (averaging response mode) when the stimulus pair had a modest direction difference ($\Delta\phi$) When $\Delta\phi$ was enlarged first saccades were either directed near the green or the red spot (bistable response mode) In a second series of experiments different instructions emphasizing either speed or accuracy of response have been given to investigate the relation between saccade accuracy and latency It appears that independent of instruction there is a fixed relation between saccade metrics and latency The only way to avoid errors, such as averaging responses is to delay the saccade Hypothetical mechanisms underlying this relation are discussed against recent neurophysiological studies

Saccade metrics Saccade latency Target selection Colour discrimination Human

INTRODUCTION

When two visual targets, having a small eccentricity difference (ΔE), are simultaneously presented along the horizontal axis at one side of the fixation point, the response of the saccadic system is usually directed in between the two stimulus positions (Findlay, 1982) In an earlier study (Ottes *et al*, 1984), where two equally eccentric spots were presented simultaneously on different meridional axes (difference in direction $\Delta\phi$), the same *averaging* phenomenon occurred if $\Delta\phi$ was sufficiently small, e g 30 deg When $\Delta\phi$ was enlarged, e g to 90 deg, a clearly *bistable* response was observed the saccade ended near one or the other stimulus This bistable response mode of the saccadic system has been reported earlier for simultaneous double stimuli on opposite sides of the fixation point ($\Delta\phi = 180$ deg, Levy Schoen, 1969, Findlay, 1980) In our previous paper the same saccade response mode could be demonstrated with double spots confined to one half field, both with large separation $\Delta\phi$ stimuli as well as with large separation ΔE stimuli (Ottes *et al*, 1984)

A comparable change from an averaging to a bistable response mode could also be shown using *double-step* stimuli (Ottes *et al*, 1984) In these experiments the first stimulus step was 15 deg to the right (or left) When the second step increased target eccentricity by another 15 deg, the majority of saccades in a certain latency range with respect to the second displacement ended in between the initial and the final target position This confirmed earlier studies (Becker and Jurgens, 1979, Van Gisbergen *et al*, 1981) When the second step was made very large (e g 45 deg), short-latency responses were again directed near the first location and late saccades brought the gaze directly to the final target position However, in this condition there was an intermediate range of response delays where either of these saccade types could occur, but almost no averaging responses appeared, i e the system behaved in a bistable manner

The impression gained from this earlier work is that the saccadic system shows a clear *bistable* response mode when confronted with double stimuli which are sufficiently separated If the alternatives are close together the *averaging* reponse mode occurs

So far, our evidence for the averaging in responses to double stimuli was obtained with a stimulus consisting of two identical targets To discourage the adoption of a preconceived strategy in double-spot trials, the double-spot stimulus had a short duration and was presented rarely and unexpectedly (It appeared for 250 msec in 10% of all randomly ordered trials) The averaging responses had latencies as short as single-spot saccades (Ottes *et al*, 1984) indicating that they were not the result of some time-consuming strategy adopted by the subject In these earlier experiments no explicit instruction pertaining to the double stimuli was given We have wondered whether the averaging response can be somehow related to this lack of an explicit instruction To explore the effect of instruction, and to remove any ambiguities inherent in our earlier experi-

ments, we have designed a *target/nontarget* paradigm with a double stimulus consisting of a green target and a red nontarget This paradigm is used in the present paper

In the first series of experiments (Experiment 1) double stimuli were presented rarely and subjects got the instruction to track the green spot as quickly as possible and to ignore the red spot We have obtained qualitatively similar results as in the earlier work discussed above When the difference in direction of the double stimulus is small, the response still shows averaging, even though the stimulus now consists of a target and a nontarget, and its latency is still very short When $\Delta\phi$ is a large, we find a bistable response Thus Experiment 1 leads us to the conclusion that the two response modes discussed above persist when an unambiguous paradigm is used

The large number of incorrect saccades, i e those betraying the influence of the red nontarget spot, is perhaps not so remarkable in view of the very short latencies observed It surprises us, however, that in Experiment 1 we see almost no signs of the improvement in saccade accuracy with latency, which has been reported in the literature (Findlay, 1981, Viviani and Swensson, 1982) Therefore, in a second series of experiments reported in this paper (Experiment 2), we have investigated how accuracy in this task can be improved In Experiment 2 subjects have either been instructed to emphasize the speed or the accuracy of their first-saccade response The large data set obtained has allowed us to reconstruct the relation between response latency and accuracy over a large latency range This relation shows that the only way for the system to avoid errors in the task is to delay the saccade until at least 300 msec after stimulus onset

EXPERIMENT 1

Methods

Visual stimuli were rear projected on a translucent screen, which had a background luminance of 1 2 cd/m^2 and was placed at a distance of 57 cm The green (Kodak Wratten filter no 58) target spot had a diameter of 2 0 deg and a luminance of about 5 cd/m^2 The nontarget consisted of a red (Kodak Wratten filter no 25) spot with the same diameter Its luminance was adjusted within 0 1 log units until it appeared equally bright as the green spot in foveal vision We are aware that such a brightness match between differently coloured stimuli is difficult to make Nevertheless, the obtained settings appeared to be the same across subjects and were stable from session to session within 0 1 log units The match was made only to assure that both stimuli had roughly equivalent brightnesses Accordingly, in these experiments there is no guarantee that the target/nontarget discrimination was based on colour alone A subtle luminance difference may have been present and may have been used as an additional cue, but this does not detract from the validity of our conclusions We have ascertained that colour discrimination between the red and the green stimulus, at the eccentricity where they were presented (20 deg), could easily be done by both subjects It was further established that both spots had a luminance about 1 7 log units above their detection threshold at the same eccentricity The spots were moved by way of computer controlled mirrors Fast (2 msec) shutters were used to extinguish the spots during each movement

Two subjects (J V G and F P O), with clinically tested normal colour vision (Ishihara test, Nagel anomaloscope), got the instruction to track the green target spot as quickly and as accurately as possible and to ignore the red nontarget spot No feedback on performance was given The subject's head was stabilized by a deep bite board and a head rest, vision was binocular

All 80 trials of each stimulus sequence started with the central presentation of the target After an interval with a random duration varying from 800 to 1400 msec, this central stimulus was switched off and the screen was blank for 12 msec In the great majority of trials (72 80) this gap was followed by the reappearance of the target at an eccentricity (E) of either 10, 20 or 30 deg and a direction (ϕ) which, taken relative to the horizontal axis to the right, was 0, 30, 60, , 300 or 330 deg In randomly interspersed double-spot trials (8/80), target and nontarget spots were presented simultaneously Peripheral presentations in all trials had a duration of 2 sec and were followed by a pause of 1–3 sec during which there were no spots on the screen The positions of target and nontarget were fixed in all double spot trials during one sequence Their eccentricity was always 20 deg

In the four configurations, in which $\Delta\phi$ was 30, 45, 60 or 90 deg, their locations were symmetrical relative to the horizontal axis In the $\Delta\phi = 180$ deg configuration they were presented along the horizontal axis, one at the right and one at the left To be able to compare the double-spot responses with those made to single-spot stimuli at the same locations, each sequence contained single-spot control trials, four at the green spot location and four at the position of the nontarget Differently ordered sequences were presented up to eight times per configuration to each subject over a period of three months Sessions had a duration of up to one hour and contained about 400 stimuli

Eye-movement recording

The horizontal and vertical component of the movements of the left eye were recorded with an improved version of the double-magnetic induction method (Bour *et al* , 1984) which permits a measuring range of about 30 deg in all directions and has an accuracy of 0 25 deg, or better, up to 25 deg The eye-movement and spot-position signals were filtered (−3 dB at 150 Hz) and digitized with a precision of

12 bits over a range of 100 deg and with a frequency of 500 Hz for each signal. These data as well as the changes in shutter and stimulus positions were stored in computer files for analysis. The nonlinearity in the raw eye position data was corrected off line as described by Bour *et al.* (1984). Saccade detection was performed by a computer program and was checked subsequently by visual inspection of the eye-movement record together with the detected onset and offset moments. Saccade latency was defined as the interval between the appearance of the peripheral target and the onset of the saccade.

Results Experiment 1

First-saccade trajectory. To show the spatial variability in the response, we have plotted the trajectories of typical eye-movements made to various double-spot stimuli with a $\Delta\phi$ of 90 deg (Fig. 1). Responses to the single-spot control stimuli, interspersed in a sequence with target/nontarget trials, are depicted in panel A. These eye movements consisted of a large initial saccade, mostly followed by one or more correction saccades. The first saccades in response to double-target stimuli (two green spots), the paradigm used in our previous paper (Ottes *et al.*, 1984), ended mostly near one or the other spot and rarely in between [Fig. 1(b)]. These responses were observed again in the present target/nontarget task [Fig. 1(c,d)], which implies that many first saccades were not made in the direction of the target spot. It should be noticed, that the great majority of these errors were corrected by a second saccade. We regard

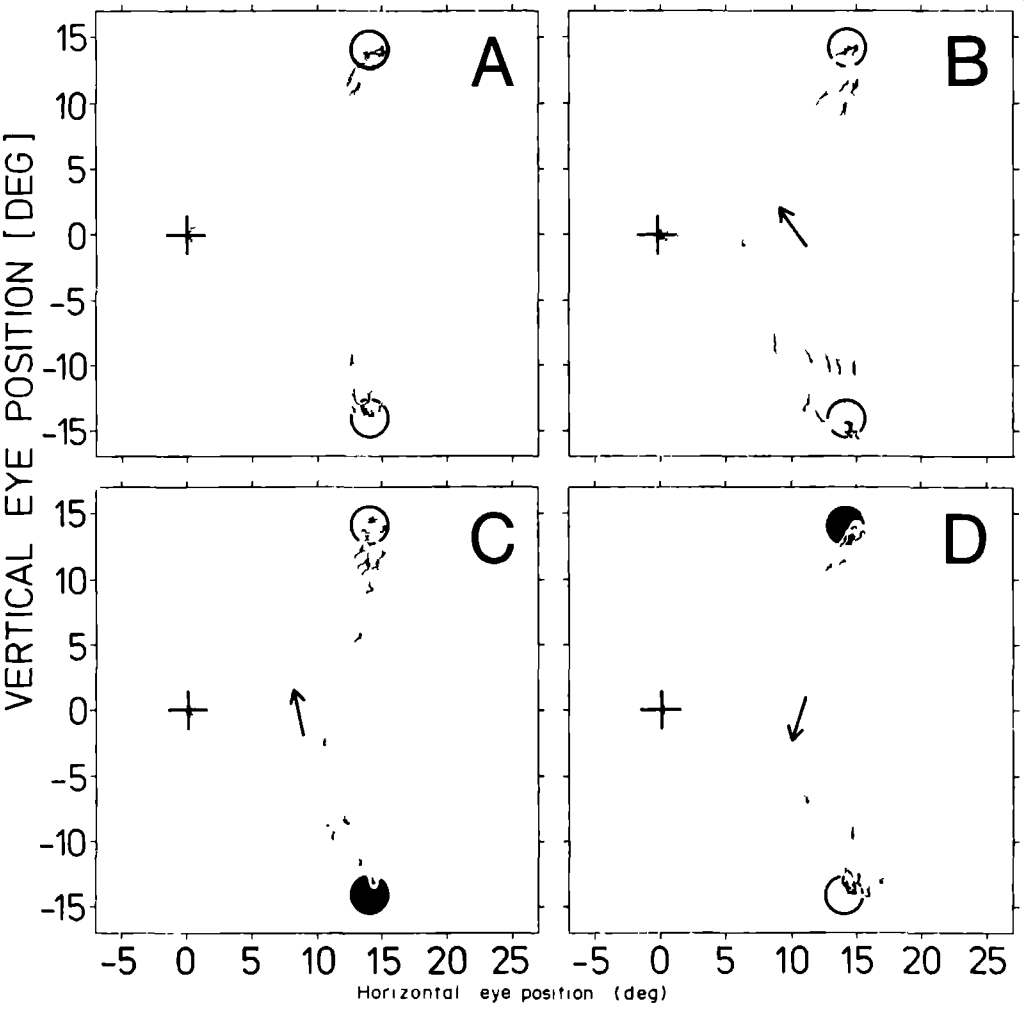

Fig. 1. Trajectories of eye movement responses from subject J.V.G. Each panel shows eight responses, superimposed on the stimulus with which they were evoked. Symbols denote the positions of the central fixation spot (cross), the green target spot (open circle) and the red nontarget (solid circle) The dots represent the eye position samples recorded over an interval of 900 msec after the onset of the peripheral target Scaling is relative to eye position at the moment of stimulus onset. Responses in panel A were made to single-spot stimuli during one target/nontarget sequence (Experiment 1). The eye movements shown in panel B were made in response to double stimuli with two identical green targets during the previously reported experiments (Ottes *et al*, 1984) In panels C and D responses to target/nontarget trials of the present Experiment 1 are shown. Panel D contains a very exceptional eye movement response consisting of a correctly directed but short first saccade, a wrong second saccade and a third vertical saccade finally bringing the gaze on target The arrows point at extremely curved saccades (see Text).

this as a sign that the subject was not simply ignoring the instruction to track the green spot

During the course of the experiments it was observed that some first saccades to double spot stimuli had an extremely curved trajectory To decide whether the curvature of double-spot responses is significantly different from what can be considered normal in oblique saccades to single spots (Viviani *et al*, 1977) we calculated the difference in direction between the initial part of the saccade (the first 18 msec) and the saccade as a whole It appeared that, in both subjects, about 10% of the double-spot saccades had a larger direction difference than control saccades These very marked direction changes in saccade trajectory were observed with the present target/nontarget paradigm [Fig 1(c,d)] as well as with the earlier double-target paradigm [Fig 1(b)]

First saccade endpoint distribution Averaging responses, characterized by a unimodal distribution of endpoints, occurring in double-target experiments with small $\Delta\phi$ value (e g 30 deg), were also found with the present target nontarget paradigm in both subjects [Fig 2 upper row (b) and (c)] As already suggested by Fig 1(c) (d) the first-saccade endpoint distribution in the $\Delta\phi = 90$ deg condition was clearly bimodal in both subjects [see Fig 2(b), (c), bottom row] This response mode is called *bistable*

The strong similarity of the response modes in the former and the present paradigm is reflected in the distribution of saccade directions This can be demonstrated with the superimposed direction histograms of single-spot and double-spot stimulus saccades in the target nontarget paradigm (Fig 3) and those in the double target paradigm (Fig 7 in Ottes *et al*, 1984) Responses with intermediate $\Delta\phi$ (45 or 60 deg) cannot be classified unambiguously upon the shape of their histogram as either averaging or bistable This suggests that the transition is gradual, rather than abrupt (Ottes *et al*, 1984)

In comparing the degree of averaging in responses to target nontarget stimuli with different $\Delta\phi$ values, we noticed that some configurations yield a very

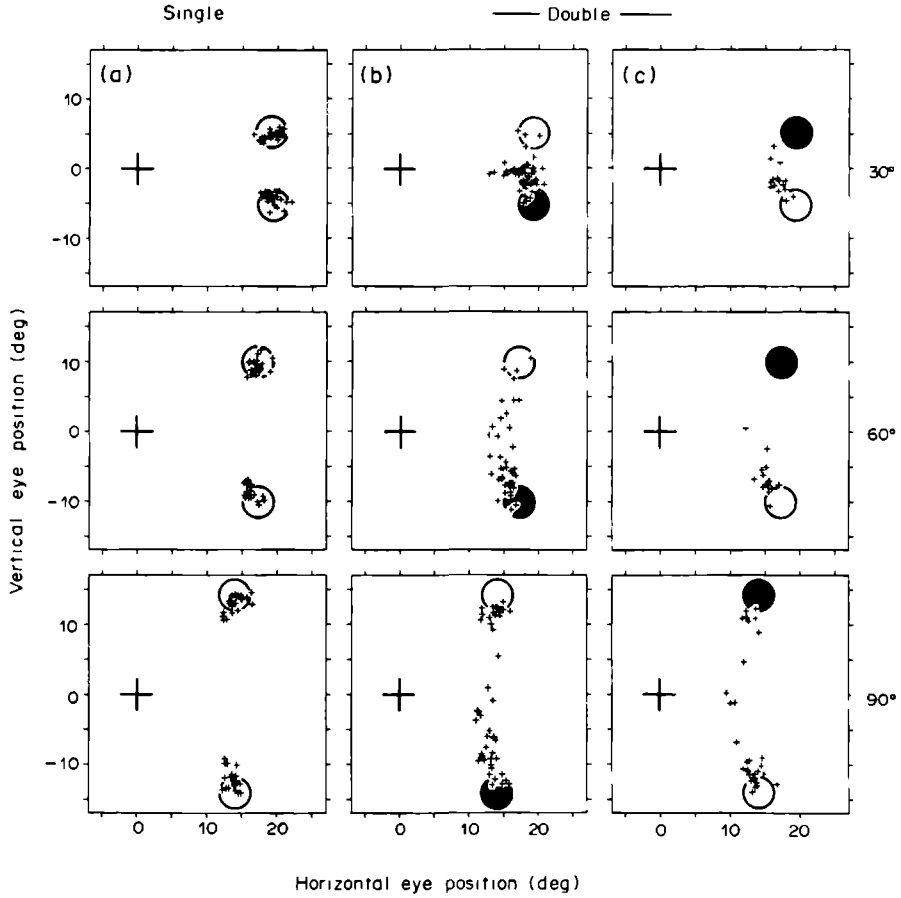

Fig 2 Each plot shows the endpoints of all first saccades of subject J V G in response to various stimulus configurations Spot positions are denoted by same symbols as in Fig 1 The endpoint of each saccade is relative to its onset position The upper row shows data recorded during target/nontarget experiments with a $\Delta\phi$ of 30 deg, in the middle row panels this parameter is 60 deg while it is 90 deg in the lower row of panels The panels of column B contain the first saccade vectors of responses to a double stimulus where the target is at the upper spot position In the stimulus of the panels in column C the target is in the lower position The saccade endpoints to both single spot control stimuli shown in column A, were obtained during double-spot experiments with the target at the upper position

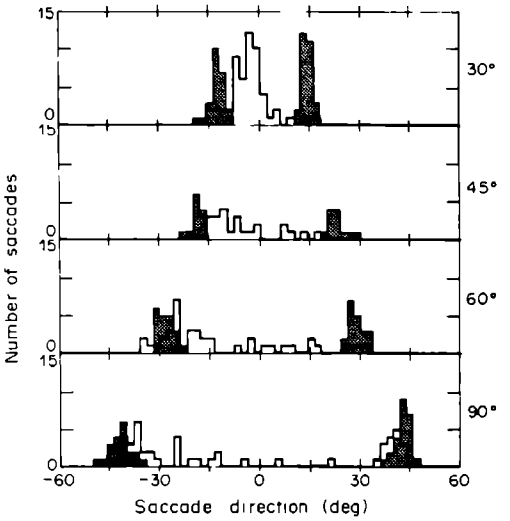

Fig 3 Histograms of directions of first saccades, made by J V G to double-spot stimuli are drawn with a bold line The two superimposed histograms in each panel obtained from both single-spot control stimuli are shaded The plots are composed from data recorded during the target nontarget Experiment 1 Each panel contains the data of responses to a double-stimulus which has a $\Delta\phi$ as indicated In all experiments the target is at the upper of the two spot positions

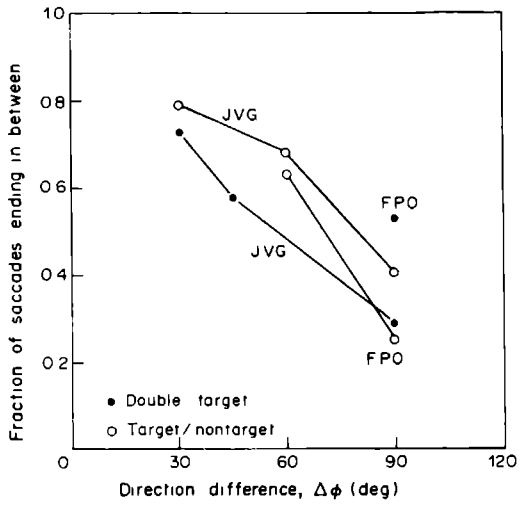

Fig 4 Fractions of averaging saccades in double-spot experiments which have a symmetrical response are plotted against the direction difference $\Delta\phi$ of the double-stimulus A saccade is defined as "averaging" if its direction is in between the two 95% ranges of the single spot response directions Data points of double-target and target/nontarget experiments (Experiment 2) are denoted by solid and open circles, respectively

skewed distribution of endpoints (see Figs 2 and 3) It appeared that this asymmetry does not depend upon a physical feature of the light spot, since it persisted when the spots were interchanged [Fig 2(b,c)] This phenomenon is reminiscent of the $\Delta\phi$ double target response distributions, which may be asymmetrical relative to the double-spot positions, even if the visual stimuli are identical (Ottes *et al.*, 1984)

The *degree of averaging*, expressed as the fraction of saccades pointing in between the two stimuli, has been plotted vs the $\Delta\phi$ of the stimulus (Fig 4) The responses to various types of double stimuli with a $\Delta\phi$ of 30 deg, as expected from Figs 2 and 3, show a large degree of averaging When $\Delta\phi$ is 90 deg, the degree of averaging is small, which is in conformity with the bistable mode of these responses Figure 4 demonstrates that the change in the degree of averaging is rather gradual, and seems to have a roughly linear relation with $\Delta\phi$ Since response distributions with strong bias (i e. with 80% or more of first-saccade endpoints closer to one than the other

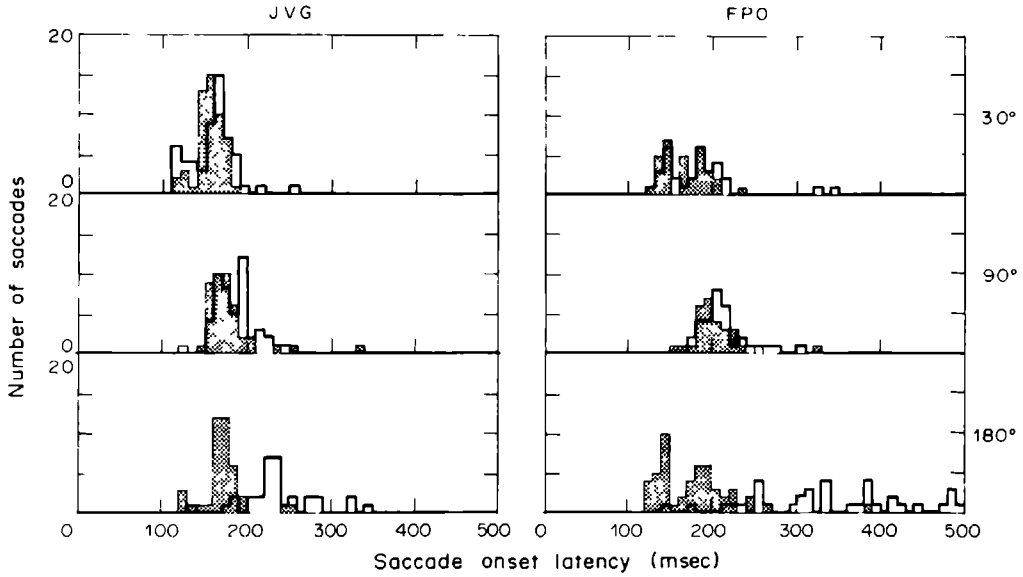

Fig 5 Histograms of latencies of first saccades made by J V G (left) and F P O (right) in response to target/nontarget stimuli during Experiment 1 The double-spot histograms are bold and the single-spot histograms are shaded The upper, middle and lower panel of each column show data of responses to stimuli with a $\Delta\phi$ of 30, 90 and 180 deg, respectively

stimulus) are difficult to interpret when one wishes to distinguish between averaging and bistable response modes (for a discussion see Ottes *et al*, 1984) these response patterns were omitted in Fig 4

First-saccade latency We investigated whether the first saccade latency depends on $\Delta\phi$ in target/nontarget experiments in the same way as it did in the previous double target experiments For small values of $\Delta\phi$, the latencies of double-spot responses were not different from those of the single-spot control responses (double-target experiments Ottes *et al*, 1984, target nontarget experiments Fig 5) This confirms our earlier conclusion that averaging as found in these responses cannot be due to the application of a time-consuming strategy Also in the present target/nontarget experiments double-target latency increases with $\Delta\phi$ This can be seen in the latency histograms of the target/nontarget data of both subjects (Fig 5) and in a plot of mean double-spot latency versus $\Delta\phi$ (Fig 6), where the latency increase in the $\Delta\phi = 180$ deg condition is quite convincing One might wonder whether perhaps latency is prolonged in all those stimulus conditions which give rise to a bimodal metrics distribution This is not simply the case although the response metrics for a $\Delta\phi = 90$ deg stimulus is clearly bistable (Figs 1–3) the latency increase effect is rather marginal (Fig 5)

Accuracy of tracking It is natural to expect that, as reported by Findlay (1981) and Viviani and Swensson (1982), tracking accuracy should improve with latency In the data of experiment 1, with rarely occurring double trials, we found very little evidence for such an increase in the accuracy of the first saccade as a function of its onset moment The average saccade-direction error, a measure for accuracy, was nearly always constant within the range of latencies, that occurred during these experiments This is shown for subject FPO in Fig 7 ($\Delta\phi = 30,60,90$), where the direction of the saccade has been plotted against its latency We found one interesting exception in the response to a

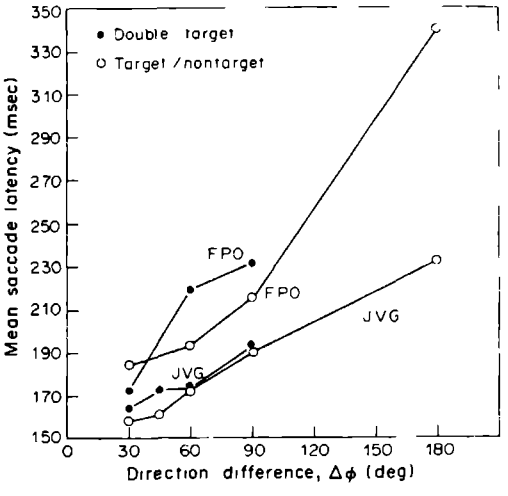

Fig 6 Mean latencies of double spot responses in experiments with double-target stimuli (solid circles) and target/nontarget stimuli (Experiment 1 open circles) shown as a function of $\Delta\phi$ The mean latencies of single spot responses in double target experiments were 186 msec (F P O) and 167 msec (J V G) in target nontarget experiments 186 msec (F P O) and 166 msec (J V G) Data points from one subject and from the same type of experiments are interconnected

$\Delta\phi = 180$ deg target/nontarget stimulus, a large scatter in latency appeared (Fig 5), whereas some early saccades were erroneously directed at the nontarget, all responses beginning 450 ms after stimulus onset or later, were correct

To investigate the factors determining first saccade accuracy, we have done a second series of experiments with a new target/nontarget paradigm (Experiment 2) We expected that by relaxing our emphasis on response speed and stressing accuracy in the instruction and by giving feedback on their performance, subjects would be able to make a larger fraction of correct responses As a further measure to ensure correct saccades, we used a high percentage of double stimulus trials to bring the system in a constant state of maximal preparedness As it will

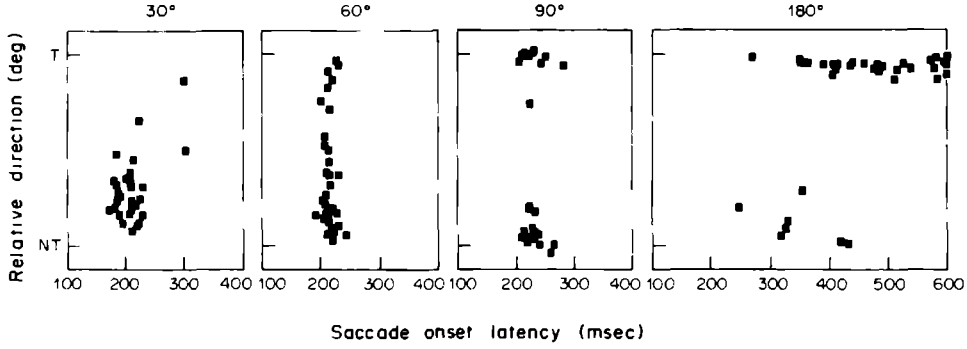

Fig 7 Relative directions of the first saccade endpoints in target/nontarget trials (Experiment 1) made by F P O plotted as a function of onset latency Because the direction of a saccade to the $\Delta\phi = 180$ stimulus was either 0 or 180 deg the horizontal amplitude of the response endpoint was used instead Data from stimuli with a $\Delta\phi$ of 30 60, 90 and 180 deg are shown in separate panels The length of the horizontal axis in the $\Delta\phi = 180$ panel has been adapted to the occurrence of very late saccades Note that some saccades towards the nontarget are exceptionally short Scaling of the vertical axis is relative to the directions (horizontal positions in $\Delta\phi = 180$) of the target (T) and the nontarget (NT)

turn out, experimental variables such as instruction and the frequency of double-spot trials do not have a clear effect on the latency-accuracy relation proper The number of wrong saccades could be drastically reduced with this paradigm but only if subjects delayed their response

EXPERIMENT 2

Methods

Experimental set-up, physical properties of the stimulus, eye-movement recording and data analysis were the same as in Experiment 1 One (J D V) of the three participating subjects (J V G , F P O and J D V) was naive, all had clinically tested normal colour vision (see Experiment 1) Two kinds of instructions were used One instruction ("FAST") was "Track the green target spot and ignore the red nontarget spot, respond as quickly after the target jump as you can" The other instruction ("ACCURATE") read "Track the green target spot and ignore the red nontarget spot Go directly to the green spot and avoid any fixation near the red nontarget as much as you can" Both instructions were further emphasized by vocal feedback After a FAST instruction, the experimenter kept reminding the subject to respond as soon as possible by warning him immediately after a late saccade During stimulus sequences preceded by an ACCURATE instruction, each incorrect response was at once reported to the subject

Stimulus

Out of the total number of 80 trials in each sequence 56 (70%) were double spots and 24 were single spots All spots were presented at an eccentricity of 20 deg In 20 double trials $\Delta\phi$ was 30 deg, an identical number of trials had a $\Delta\phi$ of 60 deg, and the remainder (16) had a $\Delta\phi$ of 180 deg The double spot positions were symmetrical with respect to the horizontal axis on the right ($\Delta\phi = 30$ deg), on the left ($\Delta\phi = 60$ deg) or the vertical axis ($\Delta\phi = 180$ deg) Each of the three double-spot configurations in each sequence occurred in two versions, obtained by interchanging target and nontarget position Four single spot control stimuli were presented at each of the six double spot positions The six types of double spot stimuli were intermingled with the single spot control stimuli in a random order in each sequence By alternating two such sequences it was made impossible for the subject to have foreknowledge about the target position in any double spot trial

It was observed in the course of these experiments that, following an ACCURATE instruction, subjects had prolonged latencies not only in double-spot trials but also in the interspersed single-spot control trials (cf Becker and Jurgens, 1979) In order to quantify this effect of instruction on latency, we measured saccadic responses in special stimulus runs where no double spot stimuli occurred Preceding these control runs, subjects were instructed to follow the target as quickly and as accurately as possible These control sequences ("Single only", Fig 11) were obtained by simply blocking the light path of the nontarget in one of the above described target nontarget sequences The single-spot control trials which were interspersed among double-spot trials in the main experiment will be referred to as "Single mixed" (see Fig 11)

Results Experiment 2

Relations between first saccade timing and accuracy As might have been expected, subjects instructed to go directly to the target (ACCURATE instruction, see Methods) were indeed able to do so but only if the saccade was delayed sufficiently long [Fig 8(b)] The FAST instruction results in Fig 8 ($\Delta\phi = 30$) as well as those obtained for the other configurations (Fig 9), show remarkably little difference from the picture emerging from Experiment 1 The $\Delta\phi = 30$ deg FAST saccades again had short latencies and often were directed in between target and nontarget Although in these runs subjects were hard-pressed to initiate their first saccade as early as possible and made many erroneous first saccades, as in Experiment 1, they did not forget to discriminate between target and nontarget in the majority of the responses which began with a wrong first saccade, the second saccade brought the eye on target Only when the longer latency ACCURATE saccades are added, does a clear relation between saccade metrics and saccade latency emerge [Fig 8(b),(c)] In the short latency range, the Experiment 2 results agree closely with earlier results, as far as the frequency of averaging saccades is concerned

The metrics of saccades to the single spot control stimuli, intermingled within the series of double spot trials [upper panel Fig 8(a)], give an idea about the accuracy with which the task can be carried out in the absence of a nontarget stimulus In this type of response there is no clear improvement in accuracy with latency The observation [Fig 8(a)] that when subjects got an ACCURATE instruction they delayed their saccades in *all* trials, although this improved accuracy only in double-stimulus trials, is interesting in itself and will be dealt with later on

Interestingly, whenever saccade latency was below about 300 msec, regardless of whether the subject had received a FAST or an ACCURATE instruction, the saccade metrics distributions as observed in Experiment 1 (see above) were found once again Almost all saccades made under the FAST instruction fell into this category and thus showed *averaging* in the $\Delta\phi = 30$ deg configuration and a *bistable response pattern* of correct and incorrect first saccades when $\Delta\phi$ was 180 deg As Fig 8(b) shows clearly for the $\Delta\phi = 30$ deg configuration, the latest FAST responses and the earliest ACCURATE responses overlap in time which provides us with a welcome

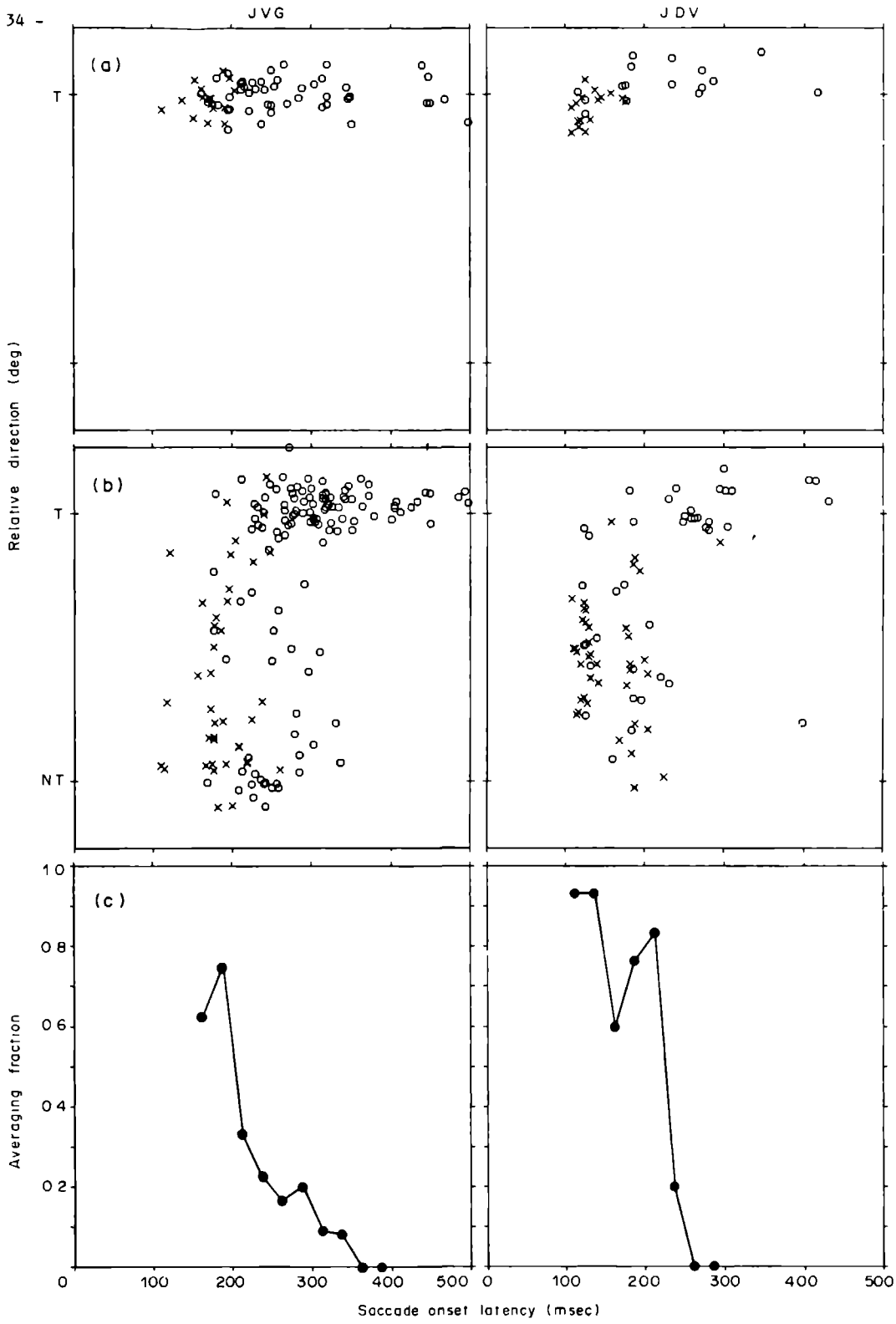

Fig 8 Direction of first saccade responses measured in Experiment 2 to single spots (row A) and $\Delta\phi = 30$ double-spot stimuli (row B) plotted against onset latency The vertical axis scaling is relative to the first saccade directions of responses to single spots at each of the double spot positions The data from the stimuli with a target direction of +15 deg have been pooled with those with a target direction of −15 deg after direction reversal of the latter responses The instruction used is denoted by symbol FAST crosses, ACCURATE circles In row C the fraction of averaging responses to $\Delta\phi = 30$ double spots, within each 25 msec latency bin containing at least 5 saccades, is plotted against mean latency of the same saccades Data in C are pooled across instruction Averaging is defined as in legend of Fig 4 Left-hand column of panels contains the data of subject J V G , right-hand of subject J D V

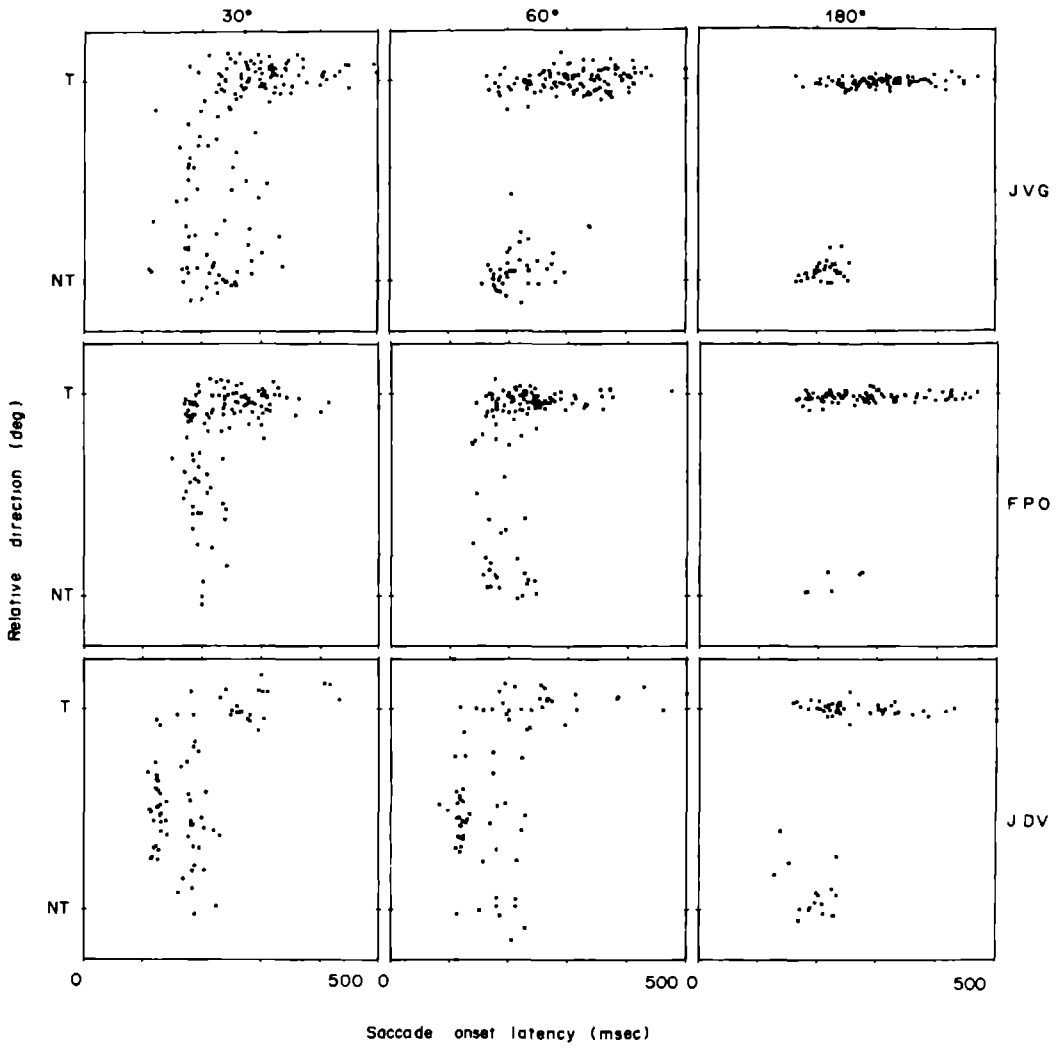

Fig 9 Relative first saccade direction (for $\Delta\phi = 30$, 60) or horizontal position (for $\Delta\phi = 180$) in double-spot responses during target/nontarget experiments (Experiment 2) Each column of panels contains the data for same $\Delta\phi$ (30, 60 and 180), each row of panels depicts the responses for one subject (J V G F P O and J D V) The vertical axis scaling is relative to the mean of the same parameter in first saccades to single spots at each of the double spot positions Data are pooled over stimulus trials with target in upper and lower position and across instruction

opportunity to check, in this latency range, whether instruction has a direct effect on the metrics distribution of saccades which does not simply reflect its obvious effect on saccade timing Since we found that FAST and ACCURATE saccades in the 200–250 msec time bin have about the same direction distribution, it seems likely that instruction can influence saccade accuracy only by affecting latency

A more complete survey of the results in all three subjects for the various stimulus configurations was obtained by pooling across FAST and ACCURATE data (Fig 9) To construct this figure (as well as Fig 8) data from trials which had identical target/nontarget positions, as well as those where locations were interchanged (see Methods), have been pooled For the response to $\Delta\phi = 180$ deg stimuli, instead of relative saccade direction, relative horizontal saccade amplitude was plotted along the vertical axis It is clear from all 9 panels in Fig 9 that saccade accuracy improves with latency The earlier data (Experiment 1, see above) as well the present FAST data simply do not span a sufficiently wide latency range to show this relationship It is equally clear from Fig 9 that early first saccades, also in these experiments where the majority of trials consisted of double stimuli, are often misdirected Their metrics distribution varies from unimodal ($\Delta\phi = 30$ deg) to bimodal ($\Delta\phi = 180$ deg) Early first saccades made in $\Delta\phi = 60$ deg trials have direction distributions somewhere in between these extremes, dependent upon the subject Some saccades in the $\Delta\phi = 180$ deg condition, which initially went in the direction of the nontarget stimulus were strongly hypometric and were, sometimes very shortly, followed by a second saccade in the opposite direction We have also seen saccades which were apparently corrected in

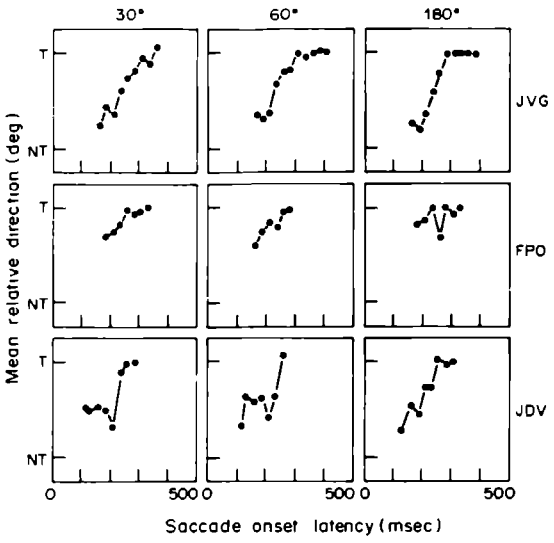

Fig 10 Mean first saccade direction (in $\Delta\phi = 30, 60$) or horizontal position (in $\Delta\phi = 180$), within each 25 msec latency bin containing at least 5 responses, is plotted against mean latency of the same saccades Data pooling and vertical axis scaling and lay-out as in Fig 9 Mean saccade direction is of course, a less than ideal characteristic when the underlying distribution is bimodal This means that most curves pre-eminently those for the $\Delta\phi = 180$ deg condition must be interpreted with caution and always in conjunction with the figure showing the original data-points from which it has been derived (i e Fig 9)

midflight, not only in the $\Delta\phi - 180$ stimulus (cf Becker and Jurgens, 1979) but also in the other double stimulus configurations (cf Van Gisbergen *et al*, 1982) These saccades with sudden direction changes were briefly discussed above (Results Experiment 1)

A better appreciation of the relation between saccade metrics and latency can be gained from Fig 10, where mean relative saccade direction ($\Delta\phi = 30,60$) or mean relative horizontal position ($\Delta\phi = 180$) has been plotted against first saccade latency The mean values were computed in adjacent 25 msec bins containing at least 5 saccades, from the data in Fig 9 At latencies beyond 300 msec the influence of the nontarget stimulus has become negligible in all subjects In the short-latency range there are minor but consistent differences among subjects in their susceptibility to nontarget stimulus disturbance These differences will be considered further in the Discussion The extremely short-latency data from subject J D V suggest that the metrics/latency relation may have a plateau before the improvement of saccade precision with latency becomes first noticeable

As far as we know, curves over the entire saccadic latency range of interest like those in Fig 10 have not been determined before Viviani and Swensson (1982) constructed what they called a speed–accuracy relationship for the saccadic system They plotted mean

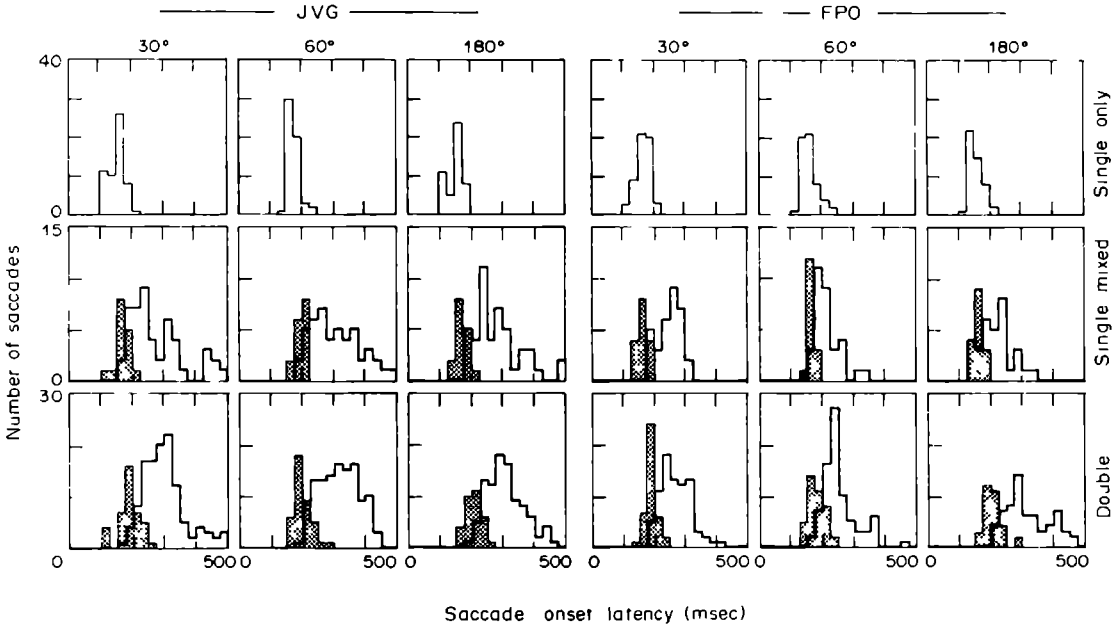

Fig 11 Onset latency histograms of first saccade responses made after a FAST instruction (shaded) and after an ACCURATE instruction (bold) The left half of the figure shows the data of subject J V G , the right half of subject F P O Data of responses to stimuli with different $\Delta\phi$ (30, 60 or 180) are depicted in separate columns The upper row shows the latency histograms of single-spot responses recorded during control runs with only single-spot trials (single only see Methods) The middle row contains the histograms derived from single-spot trials interspersed among double spot trials in the standard stimulus series of Experiment 2 (single mixed) The bottom row comprises the data of double-spot responses of the same standard series (double)

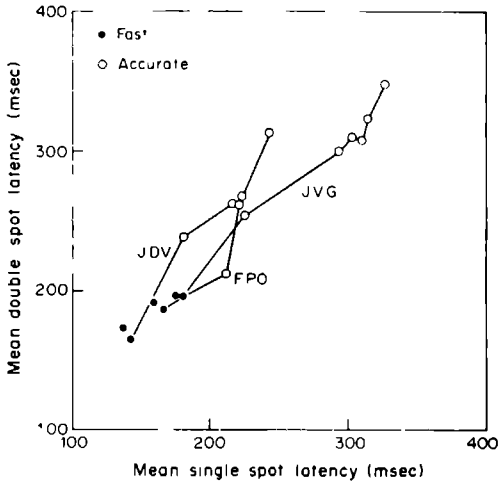

Fig 12 Mean latency of the first saccades to all double-spot stimuli in each target nontarget Experiment 2 sequence has been plotted against mean response latency in all single spot trials (single mixed see Methods) in the same sequence Data points belonging to the same subject are interconnected Data points of sequences preceded by the ACCURATE instruction are denoted by open symbols, those belonging to FAST instruction by closed symbols

error rate (error percentage) against mean latency for all saccades after each of the two instructions used, separately In this way, which is different from ours, they constructed a speed-accuracy relationship for the long-latency range

Effects of instruction and stimulus configuration on saccade timing As was already obvious from the examples in Fig 8(b), the instruction ACCURATE causes first saccades in double stimulus trials to have prolonged latencies (bold histograms in bottom row of Fig 11) The effect that subjects delay the saccade in double stimulus trials when they have received an ACCURATE instruction is completely in line with what should be expected given the fixed instruction-independent relation between saccade accuracy and latency (Fig 10) What is less easy to understand is why under these conditions latency in the intermingled single-spot trials is also clearly prolonged (see bold histograms in middle row of Fig 11) This seems odd, at first sight, since delaying a single spot saccade does not make it more accurate [Fig 8(a)] Our present hypothesis to explain this phenomenon is that the only way to delay the saccade in *certain* trials is to change a presetting which has consequences for *all* trials Apparently it is impossible to delay the saccade *selectively* in only those trials where two stimuli have been presented Some support for the idea that delaying double stimulus saccades in the ACCURATE task relies on the use of some presetting which has inevitable consequences also for latency in intermingled single-spot trials comes from data in Fig 12 To obtain this figure, mean *single* spot latency was plotted against the corresponding mean *double* stimulus latency for a number of repeated separate experimental runs There appears to be little variation in mean latency, within a given subject, under the FAST instruction By contrast, under the ACCURATE instruction, single and double stimulus mean latency shows much more variability from one run to the other, but, as Fig 12 shows, the two variables appear to be strongly correlated Since these data were obtained from fully alert subjects, there is no reason to suspect that the relation in Fig 12 is an artifact of fatigue or lack of alertness

To illustrate the effect of instruction and stimulus on latency, histograms of first-saccade latency under various conditions are shown for subject J V G (left) and F P O (right) in Fig 11 The histograms in the upper row were obtained from responses to single-spot trials in separate control sequences, where all nontarget spots had been left out (single only, see Methods) The middle row of panels in Fig 11 contains the latency data of first saccades to single-spot trials interspersed with double-spot trials in the standard sequences of Experiment 2 (single mixed, see Methods) The latencies of the double-spot responses in these Experiment 2 sequences were used to construct the bottom row of panels (double) By comparing the upper and middle row histograms in Fig 11 it can be seen that under the FAST instruction (shaded histograms) single spot latency shows little or hardly any effect of the presence of interspersed double-spot trials If the instruction-dependent increase in single-spot latency reflects presetting of saccade timing, Fig 11 suggests that subject J V G relied even more on this "strategy" than did subject F P O (Fig 11) In this context it is interesting to compare the middle and bottom row histograms in Fig 11 for the various stimulus configurations While under both instructions double-spot saccade latency shows little increase in $\Delta\phi = 30$ deg trials compared with the corresponding interspersed single-spot controls, a marked latency prolongation is seen in the $\Delta\phi = 180$ deg condition, especially in F P O This latter stimulus-induced saccade delay is clearly reminiscent of the effect observed in Experiment 1 (see Results) This property of F P O 's saccadic system may be a partial explanation of why the putative instruction-induced "preset' effect was less marked in this subject than in J V G

DISCUSSION

A striking result emerging from this and earlier studies (Coren and Hoenig, 1972, Findlay, 1981, Ottes *et al*, 1984) is that whenever the saccadic system makes a short-latency response to double-spot stimuli, its *metrics* distribution is remarkably inaccessible for modification by instruction and seems mainly determined by the relative positions of the stimuli, their sizes and intensities The remarkable result is not so much that the system is so error-prone in short latency responses, but rather that these violations of the instruction take the special form of compromising (i e averaging) responses when the two stimuli are sufficiently close together Our results

demonstrate very clearly that the averaging phenomenon described in our earlier paper cannot be attributed to a lack of a clear instruction They also show that somehow the mechanism for short-latency averaging responses seems simply immune to instruction

In line with common-sense knowledge, our data (Experiment 2) show that the timing of saccades is under voluntary control After all, it is possible to ignore the stimulus and to make no saccade at all Exploiting this capability by delaying the saccade seems to be the only possibility the subject has to avoid the averaging response pattern and to generate saccades whose metrics distribution complies with the instruction given The subjective impression, reported spontaneously by all subjects, was that delaying the saccade required a deliberate strategy Whenever the enaction of this strategy is momentarily neglected, the system seems to come in a "default-state" characterised by short-latency responses At any rate, the strong impression gained from Findlay's (1981) study and the present work is that if a preconceived strategy played any role at all in these experiments, it was essential to *avoid* rather than to *generate* averaging responses

The experiments in this report, by using different instructions, have made it possible to reconstruct the relation between saccade metrics and latency over the entire time domain of interest (Figs 9 and 10) The earlier studies of Findlay (1981) and of Viviani and Swensson (1982) had only revealed parts of such a relationship in the short- and long-latency range, respectively An interesting question, which will now be further discussed is *what mechanisms* may underly the metrics-latency relationship in the target/nontarget tracking task This problem will be discussed from two different points of view (hypotheses A and B) which are by no means mutually exclusive

POSSIBLE MECHANISMS

Hypothesis A The metrics-latency relation as a psychometric function

In order to carry out the target/nontarget tracking task, the brain must (1) detect the two stimuli and determine their retinal location (position information) and (2) identify the target (discrimination information) The system will need time to generate these signals but it is conceivable that the position information starts becoming available at an earlier point in time than the data needed for the perceptual discrimination, and furthermore, that each type of signal becomes more reliable as time proceeds One might propose, then, that the gradual improvement of saccade accuracy with latency (Figs 9 and 10) reflects the steadily increasing reliability of the discrimination information and in this sense represents a psychometric curve (Eijkman, 1979) Clearly, under our experimental conditions, the discrimination information used to guide saccades with latencies in excess of about 300 msec must have reached an asymptotic level in reliability

According to such a view, the discrimination information must have been available slightly earlier in subject F P O, whose metrics-latency relation is shifted to the left compared to similar data from the other subjects To explain the occasional occurrence of strongly curved saccades in terms of the present hypothesis, one would assume that these saccades started at the onset of the transition period when the reliability of the discrimination improves rapidly This would allow for the fact that most of these saccades curved towards the target, but why direction correction was only partial in many of these saccades [Fig 1(c,d)] is still not understood A related potential problem with hypothesis A is that it does not provide a natural explanation for the fact that in short-latency responses to the $\Delta\phi = 30$ deg configuration, the saccadic system was not simply "guessing" (i e randomly selecting one or the other stimulus spot), but showed a strong tendency for making compromise responses (averaging) One possible way to account for this is to assume that at this stage, when the discrimination information apparently is still completely unreliable or even nonexistent, the position signal likewise has very poor quality in the sense that it has low spatial resolution Such a possibility has been mentioned earlier in the literature (Findlay, 1981, Findlay and Crawford, 1983) Another problem is, why J V G, in contrast with F P O, makes most of his early saccades towards the nontarget This phenomenon cannot be explained on the basis of the psychometric function hypothesis alone

The set of data in this paper is obviously insufficient to evaluate these ideas, but new experiments, which can be done to explore them further, come readily to mind Currently, we are carrying out experiments in which the difficulty of the target/nontarget discrimination is varied By increasing its difficulty, we hope to be able to dissociate the time course in the improvement of the position information from that of the discrimination information In another series of experiments the target/nontarget discrimination is made easier, by deliberately providing an intensity cue in addition to the colour cue If hypothesis A were valid, we would expect that under these conditions the accuracy-latency relationship should shift to the left so that the error rate in the short-latency range would diminish This prediction is borne out, however, only when the red nontarget spot has a lower intensity than the target Remarkably, when the red spot is *more* intense, the error rate in short latency responses is unchanged or *even higher* than when the additional intensity cue is absent These preliminary findings seem to be at odds with hypothesis A which would lead one to expect that performance should have been better in *both* cases when the additional intensity cue was provided

Hypothesis B A dual system for the visual guidance of saccades

When taken together, data in this paper and the literature suggest that the metrics distribution of short latency saccades cannot be changed by an instruction requiring the system to make a discrimination either based on colour (present experiments) or on fine grain spatial information (Findlay, 1981) On the other hand, the metrics distribution can readily be manipulated in a stereotyped fashion, without the need for instruction, by giving the two stimuli a difference in intensity (Deubel and Hauske, 1984, Ottes *et al*, 1984) or in size (Findlay, 1980) These properties seem to point to the existence of a separate mechanism for generating short-latency saccades, which is hard-wired [see, however, Findlay and Crawford (1983) for effects of extensive training] and unable to use discrimination information The longer-latency saccades, in our experiments, guided by discrimination information, must have been generated by a different mechanism Therefore as an alternative to hypothesis A, which tries to explain our results in terms of the time-dependent properties of a *single* neural system, one might consider the following scheme (hypothesis B) We propose, that the *metrics* of visually guided saccades are controlled by a *dual* system in a parallel arrangement

(a) a short-latency subsystem, which, when several stimuli are presented, "automatically" makes a selection based on their energy content and relative timing To explain our results, we assume that this subsystem has transient response properties, poor spatial resolution and lacks feature-extracting capabilities

(b) A long-latency subsystem with good spatial resolution and the same feature-extracting capability as the perceptual system, which can be used for target selection following rules set by prior instruction or the action program of the organism

As we have noticed before, the timing of saccades appears to be under voluntary control and creates a possibility of tapping either subsystem a or b

POSSIBLE ROLE OF SUBCORTICAL AND CORTICAL MECHANISMS

Although a compelling rationalisation cannot yet be made, we think it is worthwhile to try and relate these distinctions between short-latency and longer-latency response modes of the saccadic system with the role of subcortical and cortical mechanisms in the visual guidance of saccades

Role of subcortical and cortical mechanisms

Experiments relying on single-unit recordings in trained animals, lesioning and electrical stimulation, have made clear that both cortical and subcortical areas in the brain are involved in the visual guidance of saccades Following a superior colliculus (SC) lesion, a monkey can still make visually elicited saccades but these have clearly prolonged latencies (Wurtz and Goldberg, 1971, Albano *et al*, 1982) It is interesting to note, in the context of this study, that these animals are less often distracted by irrelevant stimuli (Albano *et al*, 1982)

Monkeys with SC ablations almost completely lose the ability to make visually guided saccades after subsequent ablation of the frontal eye fields (FEF, Schiller *et al*, 1980) With the SC still intact, ablation of this cortical area has less dramatic effects

Since the lateral geniculate-striate cortex pathway is known to subserve colour and pattern vision, it is of interest for this discussion to know the effect of area 17 ablations It has been reported that humans, perceptually blind because of area 17 damage, can be induced to make visually guided saccades (Sanders *et al*, 1974) In a recent review, Campion *et al* (1983) have challenged the idea that these saccades were made without area 17 involvement Cooling experiments (Schiller *er al*, 1974) have shown that cortical and subcortical systems may interact It was found that after cooling area 17, cells in the deeper layers of the SC could no longer be driven visually

Electrophysiological studies have shed more light on the visual analysis capacity of collicular neurons Cells in the superficial layers have large receptive fields (Goldberg and Wurtz, 1972) and seem to have very little capacity to analyse the shape of visual stimuli (Cynader and Berman, 1972) In addition, these cells appear to be ill suited to analyse the spectral properties of visual stimuli (Marocco and Li, 1977) Their retinal inputs seem to lack colour-opponent signals (Schiller and Malpeli, 1977)

It is natural, then, to wonder whether the early, frequently incorrect omit, saccades in our experiments may have been mediated by the colliculus system The colour blindness (Marocco and Li, 1977) and the transient response of collicular neurons (Moors and Vendrik, 1979) make this idea attractive As we have discussed above, it is well known that short-latency saccadic responses to a double stimulus are strongly influenced by the relative size and intensity of its constituents Studies on receptive field properties of SC neurons (Goldberg and Wurtz, 1972, Stein *et al*, 1973, Sparks and Pollack, 1976, Moors and Vendrik, 1979) make it quite likely that such stimulus differences could be represented in the total population response For a discussion on how stimulus representations in the SC neural map could contribute to averaging, we refer to our previous paper (Ottes *et al*, 1984)

It does not seem unreasonable to propose that the late, correct saccades in our experiments may have been mediated cortically (area 17 and perhaps area 8) At the moment, further evaluation of the neural basis for the generation of these two groups of eye movements is hampered by the lack of electrophysiological recordings in the monkey SC under conditions as in our target/nontarget experiments Double spot stimuli have been used but not in

combination with a task to discriminate between target and nontarget (Wurtz and Mohler, 1976; Goldberg and Bushnell, 1981). Such experiments are currently being performed by our group. Furthermore, there are no behavioural data on the effects of SC or FEF ablation on the execution of a similar double-stimulus task, except for those of Albano *et al.* (1982).

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REFERENCES

Albano J. E., Mishkin M., Westbrook L. E. and Wurtz R. H. (1982) Visuomotor deficits following ablation of monkey superior colliculus. *J. Neurophysiol.* **48**, 338–351.

Becker W. and Jurgens R. (1979) An analysis of the saccadic system by means of double step stimuli. *Vision Res.* **19**, 967–983.

Bour L. J., Van Gisbergen J. A. M., Bruijns J. and Ottes F. P. (1984) The double magnetic induction method for measuring eye movement—results in monkey and man. *I.E.E.E. Trans. Biomed. Engng* **BME-131**, 419–427.

Campion J., Latto R. and Smith Y. M. (1983) Is blindsight an effect of scattered light, spared cortex, and near-threshold vision? *Behav. Brain Sci.* **6**, 423–448.

Coren S. and Hoenig P. (1972) Effect of non-target stimuli upon length of voluntary saccades. *Percept. Mot. Skills* **34**, 499–508.

Cynader M. and Berman N. (1972) Receptive-field organization of monkey superior colliculus. *J. Neurophysiol.* **35**, 187–201.

Deubel H. and Hauske G. (1984) How saccadic eye movements find their target. In *Localisation and orientation in Biology and Engineering* (Edited by Varju D. and Schnitzler H.-U.). Springer, Berlin.

Eijkman E. G. J. (1979) Psychophysics. In *Handbook of Psychonomics I* (Edited by Michon J. A., Eijkman E. G. J. and de Klerk L. F. W.), Chap. VI. North-Holland, Amsterdam.

Findlay J. M. (1980) The visual stimulus for saccadic eye movements in human observers. *Perception* **9**, 7–21.

Findlay J. M. (1981) Local and global influences on saccadic eye movements. In *Eye Movements: Cognition and Visual Perception* (Edited by Fisher D. F., Monty R. A. and Senders J. W.). Lawrence Erlbaum, Hillsdale, NJ.

Findlay J. M. (1982) Global visual processing for saccadic eye movements. *Vision Res.* **22**, 1033–1045.

Findlay J. M. and Crawford T. J. (1983) The visual control of saccadic eye movements. Evidence for limited plasticity. In *Eye Movements and Psychological Functions. International Views* (Edited by Groner R., Menz C., Fisher D. F. and Monty R. A.). Lawrence Erlbaum, Hillsdale, NJ.

Goldberg M. E. and Bushnell M. C. (1981) Behavioral enhancement of visual responses in monkey cerebral cortex. II. Modulation in frontal eye fields specifically related to saccades. *J. Neurophysiol.* **46**, 773–787.

Goldberg M. E. and Wurtz R. H. (1972) Activity of superior colliculus in behaving monkey. I. Visual receptive fields of single neurons. *J. Neurophysiol.* **35**, 542–559.

Lévy-Schoen A. (1969) Détermination et latence de la réponse oculo-motrice a deux stimulus simultanés ou successifs selon leur excentricité relative. *Ann. Psychol.* **69**, 373–392.

Marrocco R. T. and Li R. H. (1977) Monkey superior colliculus. Properties of single cells and their afferent inputs. *J. Neurophysiol.* **40**, 844–860.

Moors J. and Vendrik A. J. H. (1979) Responses of single units in the monkey superior colliculus to stationary flashing stimuli. *Expl. Brain Res.* **35**, 333–347.

Ottes F. P., Van Gisbergen J. A. M. and Eggermont J. J. (1984) Metrics of saccade responses to visual double stimuli: two different modes. *Vision Res.* **24**, 1169–1179.

Sanders M. D., Warrington E. K., Marshall J. and Weiskrantz L. (1974) 'Blindsight' Vision in a field defect. *Lancet* April 20, 707–708.

Schiller P. H. and Malpeli J. G. (1977) Properties and tectal projections of monkey retinal ganglion cells. *J. Neurophysiol.* **40**, 428–445.

Schiller P. H., Stryker M., Cynader M. and Berman N. (1974) Response characteristics of single cells in the monkey superior colliculus following ablation or cooling of the visual cortex. *J. Neurophysiol.* **37**, 181–194.

Schiller P. H., True S. D. and Conway J. L. (1980) Deficits in eye movements following frontal eye-field and superior colliculus ablations. *J. Neurophysiol.* **44**, 1175–1189.

Sparks D. L. and Pollack J. G. (1976) The neural control of saccadic eye movements: The role of the superior colliculus. In *Eye Movements—ARVO Symposium 1976* (Edited by Brooks B. A. and Bajandas F. J.). Plenum Press, New York.

Stein B. E., Labos E. and Kruger L. (1973) Determinants of response latency in neurons of superior colliculus in kittens. *J. Neurophysiol.* **36**, 680–689.

Van Gisbergen J., Gielen S., Cox H., Bruijns J. and Kleine Schaars H. (1981) Relation between metrics of saccades and stimulus trajectory in visual target tracking, implications for models of the saccadic system. In *Progress in Oculomotor Research* (Edited by Fuchs A. F. and Becker W.). Elsevier/North-Holland, Amsterdam.

Van Gisbergen J. A. M., Ottes F. P. and Eggermont J. J. (1982) Responses of the saccadic system to sudden changes in target direction. In *Physiological and Pathological Aspects of Eye Movements* (Edited by Roucoux A. and Crommelinck M.). Junk, The Hague.

Viviani P. and Swensson R. G. (1982) Saccadic eye movements to peripherally discriminated visual targets. *J. exp. Psychol.* **8**, 113–126.

Viviani P., Berthoz A. and Tracey D. (1977) The curvature of oblique saccades. *Vision Res.* **17**, 661–664.

Wurtz R. H. and Goldberg M. E. (1972) Activity of superior colliculus in behaving monkey. IV. Effects of lesions on eye movements. *J. Neurophysiol.* **35**, 587–596.

Wurtz R. H. and Mohler C. W. (1976) Organization of monkey superior colliculus: Enhanced visual response of superficial layer cells. *J. Neurophysiol.* **39**, 745–765.

MODEL-BASED DESCRIPTION OF COLLICULAR VISUOMOTOR FIELDS

SUMMARY

Electrophysiological and electrical stimulation studies in the monkey have disclosed that both the retinal surface and the metrics of saccades are topographically represented in the superior colliculus. This mapping of sensory and motor space onto the colliculus is nonhomogeneous in that the central region is overrepresented in both the visual and the motor map. Single unit studies have revealed that visual fields of collicular neurons are typically quite large and are characterized by a skewed sensitivity profile. Analyses by McIlwain (1975), in the cat, have suggested that this skewness property reflects mainly the spatial distortion inherent in the afferent mapping. In this paper we describe a quantitative model, based on a logarithmic mapping function combined with a Gaussian connectivity function in the colliculus, which can account for the extent and the shape of collicular receptive fields.

Collicular neurons in the deeper layers have movement-related bursts of activity for saccades in a limited amplitude and direction range related to their location in the collicular map. These movement fields, as visual fields, may be quite extensive and typically have a skewed profile. In our model, an efferent-mapping function is defined, which relates the locus of a population of recruited cells to the metrics of the ensuing saccade. The parameters of this function, which was taken to be identical with the afferent mapping function, were estimated from Robinson's (1972) electrical stimulation data. Based on the assumption that the population-activity profile resembles a two-dimensional Gaussian function, the shape and the size of movement fields can then be described with just 2 or 3 free parameters.

Electrophysiological data recorded from a small sample of collicular visuomotor neurons were used to illustrate the procedure, which we designed to apply our model to the experimental data. The best fit was obtained when either the mapping function or the spatial weighting function was slightly anisotropic. Suggestions on how the model could be improved and extended are offered in the Discussion.

Key words: visual fields, movement fields, visual map, motor map, model, saccadic system, superior colliculus, rhesus monkey.

INTRODUCTION

In this paper we will present a model for the spatial aspects of visuomotor transformations in the superior colliculus (SC) of the monkey. Two aspects of collicular function are of prime interest in the present context and must first be discussed briefly: the structure of collicular neural maps and the shape of collicular visuomotor fields.

The SC in the monkey is a multilayered structure. The functional properties of its neurons are strongly related to their anatomical position. In the superficial layers one finds a retinotopic map (Cynader and Berman, 1972) which is nonuniform in the sense that more central parts of the retina have an expanded representation on the collicular surface. The retino-collicular mapping characterizes the point-to-point relation which exists between the sensory surface (the retina) and the matrix of collicular neurons. The mapping specifies where each SC neuron has its most responsive retinal locus. Collicular neurons, especially those with large receptive fields, characteristically have a skewed sensitivity profile along a meridional retinal axis. This contrasts markedly with the situation in retinal ganglion cells whose receptive fields are roughly isotropic and much smaller than the large fields found deeper in the SC.

McIlwain (1975) has shown graphically, that the shape of collicular visual fields in the cat is intimately related to the spatial distortion in the nonuniform afferent mapping. Much of the variability in the shape, as well as some of the variability in size of receptive fields plotted in retinal coordinates, disappears after replotting their contours in collicular coordinates (McIlwain, 1975). Of course,

the variability in field size at a fixed retinal site cannot be accounted for by the nonuniformity of the mapping. McIlwain has suggested that these local differences may reflect variability in the spatial range of the intracollicular convergence.

In the deeper layers SC neurons show a burst of spikes which is temporally related to the onset of saccades in a limited range of amplitudes (R) and directions (Φ). In addition to this so-called movement field, these cells may have a visual field in that they may also respond to visual stimulation in a limited retinal area. The saccade-related burst is most fierce for a certain 'optimal' saccade vector (R_{opt},Φ_{opt}) and is weaker the more R and/or Φ of the saccade deviate from R_{opt} and Φ_{opt} (Sparks et al., 1976). Although they are defined quite differently, movement fields and visual fields can be plotted in a common external coordinate system. In a collicular mapping column, visual and movement fields of SC neurons may occupy identical or neighbouring positions in such a coordinate system (Wurtz and Goldberg, 1972). The mappingcolumn concept, used here merely for descriptive purposes, refers to a vertical cylinder containing all SC cells with the same (R_{opt},Φ_{opt}) value. Movement fields are also skewed in that the decay in burst rate with saccade size is more rapid for $R < R_{opt}$ than for $R > R_{opt}$. The decay in burst in burst rate which occurs as saccades have nonoptimal directions is approximately symmetrical for $\Phi < \Phi_{opt}$ and $\Phi > \Phi_{opt}$ (Sparks et al., 1976). It is known that the (R_{opt},Φ_{opt}) position in motor space, the optimal saccade, is directly related to the anatomical position of the SC neuron. One can define an efferent mapping which characterizes, as the afferent mapping in the upper layers, the topographical relation between points in an external world plane (in this case: saccade vectors in motor space) and the matrix of collicular neurons. Implicit in the concept of a motor map is the idea that, at this level, saccades are still spatially encoded (see Van Gisbergen et al., 1985). The efferent mapping has never been determined electrophysiologically in its entirety, but it is known that the visual and the motor map are, at least roughly, in spatial register (see Schiller and Stryker, 1972; Wurtz and Goldberg, 1972).

The relation between SC anatomical location and motor space has also been studied using electrical stimulation (Robinson, 1972; Schiller and Stryker, 1972). When the stimulating electrode is in the deeper layers, saccadic eye movements with R and Φ properties characteristic for each site can be evoked reliably at low current strengths. Schiller and Stryker (1972) found that saccades evoked by electrical stimulation are similar to the optimal saccade in the movement field of nearby SC neurons. It also appears that these saccades bring the fovea to a location related to the corresponding visual map position in the layers overhead (Cynader and Berman, 1972; Robinson, 1972). This description implies that the efferent mapping, too, is strongly nonuniform. Indeed, a disproportionally large amount of map space is devoted to small saccade amplitudes (Robinson, 1972). The facts described above have led to the foveation hypothesis which proposes, essentially, that signals in the upper layers caused by a visual stimulus lead to congruent motor signals in the deeper layers which bring the fovea to the stimulus which started the whole sequence of events (Schiller and Koerner, 1971; Schiller and Stryker, 1972).

So far, no attempts have been made to interpret the skewed shape of SC movement fields. Bruce and Goldberg (1985) have analyzed the shape of frontal eye field movement fields, which are also skewed. They suggest that the nonuniform mapping at earlier stages of the system (such as area 17) may have caused the skewness. In support of their idea, Bruce and Goldberg showed that while fields as a function of R were skewed, they looked symmetrical when replotted on a log R scale. In this paper we propose a model which implies a mechanistic explanation for the skewness in the shape of SC visuomotor fields. This model enables us to carry Bruce and Goldberg's idea one step further by comparing actual field data and model-based fit curves simultaneously in two dimensions. The basic purpose of this model is to provide a conceptual frame work for a quantitative analysis of the interrelations between SC map structure and visuomotor field shapes. Our scheme does not account at all for temporal properties of SC neurons. For this and other

reasons the model, whose structure and underlying rationals will now be presented, is still very incomplete.

Structure of the model

Visual receptive fields. The superficial layers in the SC receive direct input from the retina. In our model, the array of retinal nerve fibers entering the SC is topographically organized and has a homogeneously distributed density of axons over the collicular surface. By contrast, at their point of origin, their distribution is dense near the fovea and becomes progressively more sparse with retinal eccentricity (Fischer, 1973; Fig. 1A). This arrangement forms the basis for the nonhomogeneous visual afferent mapping in the SC.

We propose that each SC neuron in the superficial layers receives input from a large number of incoming afferents, such that the functional strength of these connections decays from a maximum for nearby afferents to negligibly low values for remote fibers. The simplest possibility to be considered is that, for each SC neuron anywhere in the map, input strength from the incoming fiber array can be represented by a rotation-symmetrical dome-shaped function which peaks at the position of the SC cell body. We will denote this function as the visual connectivity function.

The idea of a dome-shaped connectivity function would become rather meaningless if, in fact, only a few afferents would converge on each SC cell. Given an estimate of 110.000 optic nerve fibers (Perry and Cowey, 1984) entering a collicular surface of no more than 17 mm^2 the resulting density is at least 6500 fibers/mm^2. As will become clear below, it is not uncommon for SC neurons to have a visual connectivity function covering > 1 mm^2 of SC surface so that the number of afferent terminals for each neuron may run into the thousands.

We are aware that the assumption that all visual fields have an identical connectivity function anywhere in the SC does not account for the finding that field size increases with depth. Our intention, however, is not so much to present a complete SC model, but rather, to show how the combination of a few basic ideas may enhance our understanding of visuomotor field properties. These, after all, are the building blocks for a later more ambitious modeling attempt. To allow for the fact that neighbouring SC cells have overlapping receptive fields, their connectivity functions overlap so that each retinal afferent drives many SC cells. We like to stress that the connectivity function is an abstract notion which need not reflect the spatial extent of the neuron's dendritic field. Arborization patterns of retinal axons within the SC and intracollicular excitatory connections can extend the connectivity function beyond the dendritic field.

If the size of receptive fields of the retinal afferents, the structure of the afferent mapping and the visual connectivity function are specified, the receptivefield properties of the SC cells in our scheme are fully determined. Receptive fieldsof retinal ganglion cells increase in size with retinal eccentricity. For simplicity, we will not discuss the precise sensitivity profiles and only assume that the fields of the incoming fibers together cover the entire retina with negligible overlap. The reason why we think discussing retinal ganglion cell fields is not essential is the idea that the generally large size of SC visual fields is mainly determined by intracollicular convergence. Due to the nonuniform afferent mapping, SC neurons in our scheme have skewed receptive fields notwithstanding their isotropic visual connectivity function. This ties in with the important result obtained by McIlwain (1975) who showed that receptive field skewness reflects, to a large extent, the nonuniformity of the afferent mapping.

A further point worth emphasizing is that also the size of SC receptive fields will reflect the distortion in the afferent mapping in that the receptive fields would vary in size depending on SC anatomical location. These interrelations among afferent mapping structure, visual connectivity function and spatial properties of SC receptive fields are illustrated diagrammatically in Fig. 1 A,B. A more thorough mathematical treatment will follow (see below).

At this point it is appropriate to ask: Given the structure of the afferent mapping and a connectivity function valid for all neurons distributed in the collicular map, what is the

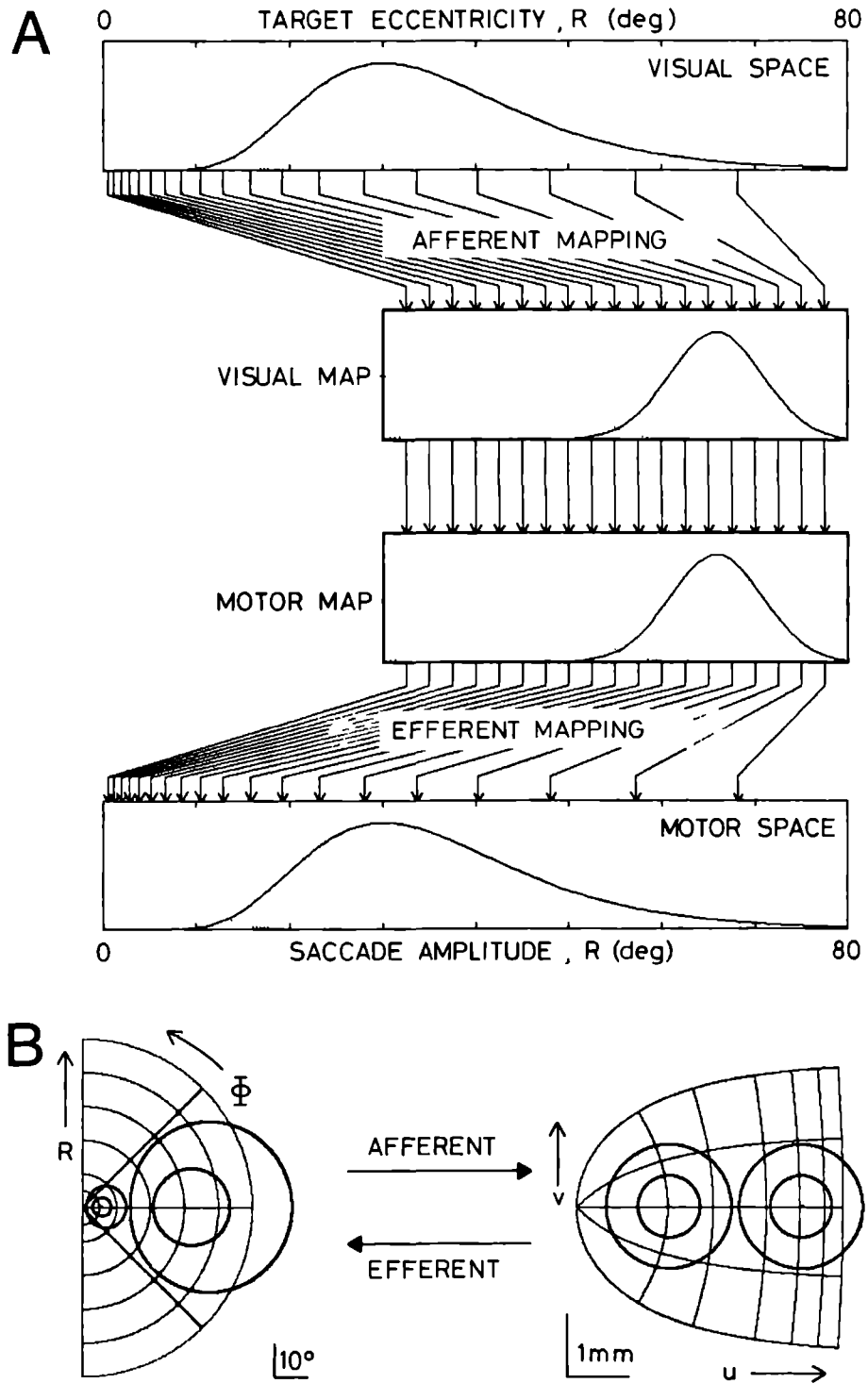

Fig. 1. General lay out of the model.
A. Because, in our model, optic nerve fibers form an equidistant array as they enter the colliculus, but not on their points of origin on the retina, the resulting visual map is nonhomogeneous. When a given SC cell receives inputs from the matrix of retinal afferents according to a Gaussian connectivity function (two curves in VISUAL MAP box), its visual field will be skewed (see two corresponding curves in VISUAL SPACE box). Since, in the model, the connectivity function is spatially invariant, the curves in the VISUAL MAP box

activity in the population of SC neurons created by a visual point stimulus? Under these conditions, this population activity profile reflects the shape of the symmetrical visual connectivity function (see Capuano and McIlwain, 1981). This should not be surprising: the broader the connectivity function, the larger the population of cells recruited by a point stimulus is going to be. That the profile of the population of cells recruited by a point stimulus and the connectivity function are precisely identical in our model can easily be shown mathematically (see Appendix I). It should be recognized that the concepts 'point image' and 'field image', introduced by McIlwain (1975), are closely related but not identical with our notions of 'population activity profile' and 'connectivity function', respectively. The reason for maintaining this distinction is that our notions are hypothetical constructs, which cannot be measured directly as such, while those used by McIlwain are the outcome of experimental procedures whose theoretical interpretation is a separate matter. In addition, it should be noted that McIlwain was interested primarily in determining contours of field images and point images whereas we, in our model, need to consider also suprathreshold activity.

The foregoing attests of the deep implications of the visual connectivity function which, together with the structure of the afferent mapping, is important for understanding receptive field properties and can serve equally well as the descriptor for the spatial distribution of activity in the array of SC visual neurons.

Movement fields. We will now discuss the interrelations between motor-related activity in the deeper layers and the metrics of saccadic eye movements. As has been mentioned before, SC movement fields typically have a skewed profile along the R dimension and the model must account for this. To understand why movement fields are skewed, we think it is essential to realize, when analysing the relation between the firing properties of a single cell and saccadic eye movements, that the latter are not caused by this particular cell alone, but by a population of cells. In the model, the population activity profile of recruited cells carrying the movement-related burst occupies different locations in the map depending on the saccade vector. The activity profile has again a dome-shaped spatial extension, which is invariant for all saccades. Variations in movement-field size within a collicular mapping column (Mohler and Wurtz, 1976) have been ignored in the model.

The orderly relation which exists between the locus of neural activity in the deeper layers and the resulting eye movement vector is the basis of the efferent mapping concept. If this mapping is to be described quantitatively, a clear definition of precisely what is being mapped is, of course, indispensible. In this

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can also be interpreted as the spatial activity profile in the population of cells created by a visual point stimulus at the corresponding position on the retina (see text). When a target leads to a saccade, the movement-related activity in the model has again a Gaussian spatial distribution centered around the same mapping column (see MOTOR MAP box). The efferent-mapping function gives the relation between the location of the recruited population of movement cells and the metrics of the resulting saccade. The lines in the figure which symbolize this nonhomogeneous topographical relationship should not be interpreted as indicating anatomical connections. The skewness and the size of movement fields (see two curves in MOTOR SPACE) is determined by the Gaussian activity profile and the efferent mapping. B. The point-to-point relationship between the external world (see halffield on the left) and the collicular maps (on the right), as seen from above, is determined by the afferent and efferent mapping functions. In the model these are the inverse of one another. The mapping function used is isotropic ($B_U = B_V = 1.5$ mm/deg; $A = 3$ deg). As a result, the distance from 0 - 80 deg eccentricity along the horizontal meridian in the map is 4.98 mm. The σ and 2σ contours of the spatial weighting function (the same asused in A) have been drawn onto the collicular surface on the right ($\sigma = 0.5$ mm). When replotted in the R,Φ coordinates of visual (motor) space, the corresponding visual (movement) fields have strikingly different sizes and noticeable skewness along the R dimension. The polar-coordinate grid on the left has meridians every 45 deg and iso-eccentricity hemi circles of 5, 10, 20, 30, 40 and 50 deg.

paper we define the efferent mapping as a coordinate transformation which assigns saccade vectors (points in R,Φ space) to centers of movement burst population activity in the SC map. Such a center, the peak of the proposed dome-shaped population activity profile for a given saccade vector, is of course embodied by the SC cell with the most fierce movement-related burst. This definition, to us, has two appealing advantages: First, since the optimal saccade for a given location in the motor map and the saccade obtained by local electrical stimulation are closely related, if not identical (Schiller and Stryker, 1972; see above), Robinson's electrical stimulation data can be used as the data base for describing the efferent mapping. Second, as we will discuss later (Discussion) our definition of the efferent mapping is fully compatible with ideas expressed by McIlwain (1976, 1982) and Sparks et al. (1976) with regard to the problem of how the firing rate of individual cells in the population may contribute to the total saccade. Since the motor map is non-uniform (Robinson, 1972), the implication is that the size of the motor vector assigned to the population activity center must be a nonlinear function of its map position when moving peripherally along the representation of a meridian. Because the efferent mapping in the model is the inverse of the afferent mapping, movement-related activity in the deeper layers, brought about by a visual target, will result in a goal-directed saccade.

If the activity in the population of movement cells has indeed a dome-shaped spatial profile, the fact that movement fields are skewed can be understood, at least qualitatively (Fig. 1A,B). When we record from a given cell while the animal makes saccades of various sizes, the associated active population of neurons will shift in the map. For both sufficiently small and large saccades, the cell will not be recruited. For the situation in between these extremes, the cell's firing rate will peak for a certain saccade amplitude (the optimum saccade for that cell). As the population profile of active cells moves to the right in Fig. 1A, saccade size will show a larger increment than the decrement in size brought about by an equal shift to the left. Because the efferent mapping is nonuniform, the effects of opposite and equal shifts in the locus of the active population on saccade size are opposite but unequal. In conclusion, the nonuniformity in the afferent and efferent mapping in our model is responsible for the skewness of visual fields and movement fields. Also with regard to field size there are interesting analogies to be noted: Since the population of active cells in the motor map is similar in all respects, except for location in the map, movement field size and saccade size will be related (Sparks et al., 1976).

There are two problems which we have sidestepped so far but need to discuss now. One point is that our discussion may have created the false impression that a clear distinction can be made between visual and motor cells. This is unrealistic: It is well established that many deeper layer cells may both have a visual receptive field and a movement field (Wurtz and Goldberg, 1972; and others). In our model the shape and the size of these visual receptive fields are again fully determined by the visual connectivity function of these neurons and the structure of the afferent map in which they are embedded.

A second, somewhat related, point is the following. When a saccade is elicited by a visual target, the movement-related discharge in the deeper layers must, ultimately, have a visual origin. The question, then, is how activity in the motor map is caused by visual signals. In our scheme vertical connections from superficial to deeper layers could subserve this function. A problem is that such connections have not been shown anatomically (see, however, Mooney et al., 1984). In our model we leave open how precisely visual signals cause the motor-burst activity. We think it would be ill-advised to be very specific about a process, from which little is known, but is likely to be rather complex. As an illustration, think of a liminal target stimulus which sometimes attracts a saccade and sometimes does not. The associated weak visual signals in some trials will create full-blown motor activity and none or less in others (Sparks, 1978). This example illustrates already that the coupling with the stimulus could be rather loose and may involve strongly nonlinear signal processing ('decision making').

For present purposes two assumptions suffice:

(1) the population motor activity is centered in the same collicular mapping column as the visual activity (Fig. 1A);

(2) the spatial distribution of the motor activity is dome-shaped just as the visual activity. If the width of the motor activity dome function should be different from the visual population activity profile, a possibility which we do not exclude, visual fields and movement fields would have different sizes (Wurtz and Goldberg, 1972).

If our model is correct, the site of maximal retinal sensitivity in the visual field and the 'optimal saccade' in the movement field of a given visuomotor cell should correspond precisely. Whether or not this is in accordance with the facts cannot be deduced from the literature. We will check this point in our own small sample of SC cells (see below).

We acknowledge that visual signals from extracollicular origin (e.g., area 17, area 8) may be important in generating movement-related activity in the deeper layers. As long as the activity which results from these other inputs conforms to the restrictions inherent in our assumptions (see above) the precise origin of the visual signals is irrelevant from the standpoint of our model. We point out that these other potential sources of visual information may have undergone the same type of afferent mapping distortion as the SC superficial layer system (see Discussion).

To summarize, the spatial properties of visuomotor cells in the deeper layers are fully characterized, in our model, by four functions:

(1) the visual connectivity function. For a given afferent-mapping function, this function determines the size and shape of visual fields in the entire array. In our model its shape can be equated with the activity population profile resulting from a visual point stimulus.

(2) the motor activity population profile. This function describes the movement-related activity in the population of SC neurons.

(3) the afferent mapping function, describing the point-to-point relation from retinal to collicular loci.

(4) the efferent mapping function, which determines the relation between the site of movement-related activity in the motor map and the metrics of the resulting movement.

To make the scheme more explicit and suitable for computer simulations, so that its properties can be confronted with experimental data, these functions will now be put in the form of mathematical expressions.

Mathematical formulation of the model.

A. Afferent and efferent mapping function.

As has been mentioned above, the structure of both the visual and the motor map in the SC of the monkey have at least a superficial resemblance with the topographical organization in area 17 of the same animal (Daniel and Whitteridge, 1961; Van Essen et al., 1984). This has prompted us to try the complex logarithmic mapping function, which has shown to be useful for describing the monkey area 17 map (Schwartz, 1980), also for describing the SC map structure. Although, given the direction of signal flow, the afferent and the efferent mapping are really the inverse of one another (Fig. 1B), we find it easier to ignore this point momentarily and to consider both as mappings from the external world to intrinsic SC coordinates. This has the overriding advantage that the same mathematical formalism can be used for both and that the degree of similarity in both maps can be compared directly.

To describe the mapping structure mathematically, a coordinate system must be chosen in the external world space (retina, motor space) and in the SC. For calculations we use a polar coordinate system in the former (R = retinal eccentricity or saccade size; Φ = retinal meridional angle or saccade direction) and a Cartesian coordinate system (u,v) in the latter. In the collicular coordinate system, defined in a plane parallel with the surface, u represents the axis along the representation of the horizontal meridian (horizontal saccades). The orthogonal coordinate, the v axis, intersects the u axis at the center of the foveal representation (u=0, v=0). Since Robinson's data suggest that the efferent mapping is somewhat anisotropic, we have used a logarithmic mapping function which is general enough so that it can cope with this complication. The mapping function used projects retinal or eye

movement coordinates (R and Φ), onto corresponding collicular coordinates u and v as follows:

$$u = B_u \ln\left(\sqrt{R^2 + A^2 + 2AR\cos\Phi}\right) - B_u \ln A \quad (1)$$

$$v = B_v \operatorname{atan}\{(R\sin\Phi) / [R\cos(\Phi) + A]\} \quad (2)$$

where:

B_u = a scaling constant determining the size of the collicular map along its u axis (mm/deg),

B_v = a scaling constant determining the size of the collicular map along its v axis (mm/deg),

A = a constant which, together with the ratio B_u/B_v determines the shape of the mapping (deg).

The term $-B_u \ln A$ is needed to ascertain that the fovea is projected on the origin (u=0,v=0) of the neural map. When $B_u = B_v$, the mapping is isotropic and the model is exactly equivalent with the complex logarithmic mapping $\vec{w} = B \ln(\vec{z} + A)$ used by Schwartz (1980) in monkey area 17. It is sometimes useful to have expressions which describe the reverse mapping from collicular to external world coordinates. These are given in the Appendix II.

B. Visual and motor population activity functions

Within the SC the dome-shaped functions discussed above (section on structure of the model) take the form of a rotation-symmetrical 2-D Gaussian weighting function:

$$W = W_{back} + W_{max} \cdot \exp\left[-\frac{(u-u_c)^2 + (v-v_c)^2}{2\sigma^2}\right] \quad (3)$$

and W = 0

for positions outside the SC,

where:

W_{max} = the peak firing rate in the population (spikes/sec),

W_{back} = background firing rate (spikes/sec),

(u_c, v_c) = location of most active SC cell in population (mm),

σ = parameter determining decay rate of rate of neural activity in the population with distance from, (u_c, v_c) in SC map (mm).

When the weighting function W is used for describing the underlying connectivity function (for visual neurons; see above), W_{max} symbolizes the functional strength of the strongest afferent input (spikes/sec) to the neuron at location (u_c, v_c) in the SC map and σ is a para- a parameter determining the decay rate of afferent input strength with distance from (u_c, v_c).

In some simulations (Fig. 4B) we allowed the intracollicular weighting function to have different widths in the u and v direction:

$$W = W_{back} + W_{max} \cdot \exp\left[-\left(\frac{(u-u_c)^2}{2\sigma_u^2} + \frac{(v-v_c)^2}{2\sigma_v^2}\right)\right] \quad (4)$$

and W = 0

for extra collicular positions,

where:

σ_u and σ_v determine the width of the weighting function along the u and v dimension in the SC, respectively. The ratio σ_u/σ_v determines the degree of anisotropy in the weighting function. When this ratio equals unity, equation (4) becomes equivalent with equation (3).

Formula (4) permits only a special form of anisotropy, namely with the long axis of the ellips along either the u or the v axis. For a more general form with the long axis in any direction a more complicated formula, with more parameters, would be needed (cf. Schwartz, 1984).

METHODS

Procedure to estimate mapping function parameters

Data published by Cynader and Berman (Fig. 9, 1972) and by Robinson (Fig. 4B, 1972) were used as the data base for parameter estimation. On an enlarged photograph of each figure the u-axis (see Introduction) was drawn through the representation of the horizontal meridian. The u-axis in the Cynader and Berman map, where the representation of the horizontal meridian is somewhat curved, is the best fit line, drawn by eye. In the case of the Robinson motor map no such problem was encountered. A further decision which had to be made concerns the location of the v-axis, which is perpendicular to the u-axis and intersects it at the point re-

presenting (R=0 , Φ=0). This point is known in the Cynader and Berman visual map but is absent, strictly speaking even undefined, in the motor map. The point corresponding with (R=0, Φ=0) in the Robinson map was determined provisionally by extrapolation (see also below).

Subsequently, u and v coordinates of each point in both maps were digitized using a

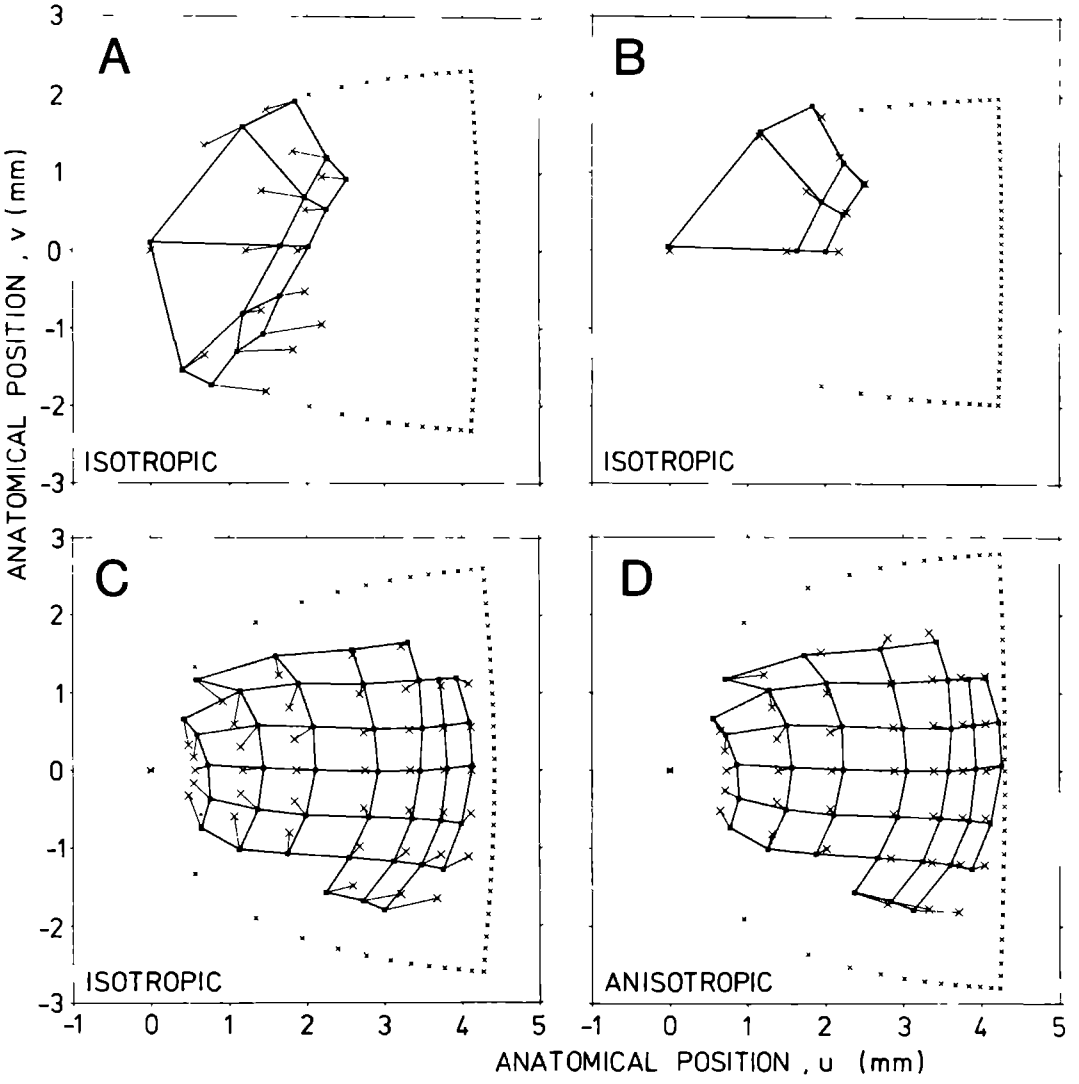

Fig. 2. Parametrization of visual and motor map data.
In all panels the point corresponding with R=0 is represented at (u=0, v=0). Data points are denoted with square symbols and are interconnected by straight bold lines. The corresponding mathematical mapping function points are denoted by a large cross symbol. The sum of squared distances between data and model map points (indicated by thin lines) was minimized. The collicular boundaries taken as the vertical meridian and the 60 deg iso-eccentricity line after transformation with the best-fitting function are shown by small crosses at 5 deg Φ and R increments. For summary of best fit parameters obtained, see Table I. A. Best fit for complete visual map data set from Cynader and Berman obtained with isotropic-mapping function. B. Best fit for upper quadrant data from Cynader and Berman obtained with isotropic-mapping function. C. Best fit for Robinson's motor map data obtained with isotropic-mapping function. D. Improved fit for same data as in C by allowing mapping function to be anisotropic.
N.B. The retinal positions of Cynader and Berman's datapoints form a regular grid in H,V coordinates (H=0,5,10; V=-10,-5,0,5,10). The retinal coordinates of Robinson's datapoint form a grid in R,Φ coordinates (Φ=+60: R=5,10,20,30; Φ=+40,+20,0,-20,-40: R=2,5,10,20,30,40,50; Φ=-60: R=20,30,40).

Table I: MAPPING PARAMETERS

data base	number of data points	mapping function	B_u (mm/deg)	B_v (mm/deg)	A (deg)	mean absolute error (μm)
Cynader and Berman (1972) (whole map)	15	iso	1.6	1.6	4.2	420
Cynader and Berman (1972) (upper half)	9	iso	1.3	1.3	2.2	110
Robinson (1972)	42	iso	1.8	1.8	5.3	240
Robinson (1972)	42	aniso	1.4	1.8	3.0	190

Table I. Optimal values for parameters B_u, B_v, and A obtained with isotropic (iso) and anisotropic (aniso) mapping function.

Summagraphics digitizing tablet connected with a DEC 11-45 computer. The tablet had a position accuracy of 0.1 mm. Since Cynader and Berman gave the relation between collicular coordinates and retinal locations in a Cartesian coordinate system whereas our model [equations (1) and (2)] is based on a polar retinal coor dinate system, the retinal coordinates corresponding with each point in the visual map were converted into polar coordinates.

The procedure to estimate the optimal parameters to fit each map was as follows. The computer, using equations (1) and (2), generated a collicular map based on a first guess of parameters. Subsequently, an iterative search based on the method of steepest descent began. The best fit was defined as the set of parameters B_u, B_v and A for which the sum of squared distances from actual map point coordinates (u,v) to the corresponding model coordinates was minimized. A property of the logarithmic mapping function [equations (1) and (2)] is that a change in B_u, B_v, or A both changes the shape of the collicular map and shifts its point of origin. Since our purpose is only to characterize the shape of the map, not to account for its precise location in the brain, the computer program had a provision to bring actual and computed map in spatial register as precisely as possible by shifting the computed map. This possibility to shift the whole map along both the u and v axis, by amounts u_o and v_o, means that a wrong provisional choice of the point (u=0, v=0) in digitizing the Robinson map (see above) will be corrected in the fitting procedure by selecting an appropriate compensatory u_o value based on the overall fit.

Procedure to fit the measured visuomotor fields

According to the model, the shape of visual and movement fields is determined by the mapping function and the collicular weighting function, W. The experimental field data consists of a list of firing rates measured in a certain time interval (see below) for a set of points in R,Φ space. To parametrize a given data set, the parameters of the mapping function were first chosen and kept fixed. The weighting function parameters W_{max}, u_c, v_c and σ (in case a circular weighting function was used) were then varied by the computer in order

to minimize the difference between measured and model-derived firing rates using a mean square-error criterion. To compute the firing rate associated with a set of weighting-function parameters for a particular point in R,Φ space, these coordinates were entered in equations (1) and (2) to find the corresponding collicular coordinates. Subsequent application of equation (3) [circular weighting function] or (4) [elliptical weighting function; see above] then yielded the desired model prediction. This procedure may be applied on visuomotor fields scanned in any random way, and not only on fields scanned along a meridian and a circle, like in this paper (see below). The term W_{back} in equations (3) and (4) was intended for the possibility that cells may have a steady, R and Φ independent, background rate (Bruce and Goldberg, 1985). In our present data set, however, no such phenomenon was noted and W_{back} was kept at zero.

In a total of 37 cells we did an R-scan experiment (12 cells), a Φ-scan experiment (14 cells) or a combination of both (11 cells). For an explanation of how these experiments were conducted we refer to the next section of the Methods. In this paper we will only use the combined R and Φ scan data. In principle, these experiments could have yielded data on 11 visual fields and 11 movement fields. The actual number is less either because the scan missed an important portion of the field, or because the responses were so noisy that no clear field profile could be discerned. In these cases the parameters proposed by the fit program had large uncertainty intervals associated with them. The uncertainty interval is a measure of how changing a parameter from its optimal value influences the goodness of fit. If a parameter has a precisely-defined optimal value, the uncertainty interval is relatively small. The data to be discussed in the Results are from five cells with both a visual and a movement field, two cells with only a visual field and one cell with only a movement field.

Electrophysiological experiments

Two rhesus monkeys were trained to refixate a target spot after it jumped from a central fixated position to a peripheral position. The animals, which had been water deprived for 16 hours, were rewarded with apple juice when on target. The monkeys underwent three separate operations under halothane-nitrous oxide anesthesia and aseptic conditions:
1) A crown (Friendlich, 1973) was attached to the skull with medical bone screws (Synthes). The crown served to immobilize the head during the experiments. 2) A gold-plated thin copper ring was implanted beneath the conjunctiva on the right eye using the surgical technique described by Judge et al., (1980). This ring was used to record eye movements with the double-magnetic induction method (Bour et al., 1984; see below). 3) A closed stainless-steel chamber, its axis directed at a point between the two superior colliculi, was implanted over a hole trephined in the skull. During each operation end-tidal CO_2, heart rate and body temperature were continuously monitored.

During electrophysiological experiments a tungsten microelectrode (Bak Inc.), having an impedance of 0.8 - 1.5 MΩ at 1 kHz, was lowered inside a guide tube through the dura. The microelectrode signal was amplified (Grass P16 preamplifier) and monitored on a storage oscilloscope. Action potentials of isolated units were discriminated from background noise by level detection and their moments of occurrence, timed with 0.1 msec precision, were stored in the computer. The entry of the SC, as the electrode was lowered slowly under hydraulic control, was heralded by clear responses to visual stimulation. In line with numerous earlier reports, cells with movement-related activity were encountered deeper in the SC.

Visual stimuli were rear projected on a translucent screen which had a background luminance of 1.2 cd/m^2 and was placed at a distance of 57 cm. The green target spot had a diameter of either 0.4 or 0.9 deg and a luminance of about 5 cd/m^2. Vision was binocular.To locate the field of a neuron, the target was presented in a random sequence at each of 49 positions in a relevant sector of the visual field (field scan). In this sector, 7 eccentricities were tested at each of 7 meridional angles. The range of the field scan could be adapted independently in the R and the Φ direction to fit the need for any particular cell. Each trial of the field scan started with the presentation of

the target at the primary position, which had a duration of 0.8 to 1.8 sec. Then the central spot was switched off, and after the screen was blank for 12 msec, the target reappeared at one of the 49 peripheral positions. At each peripheral position, the spot remained stationary for 2 sec until it was extinguished and the intertrial pause (duration 1-2 sec) began. To investigate the field further, stimulus sequences could then be run which were limited to 7 equidistant positions along a meridian through the estimated Φ_{opt} value of the field (R-scan) or to 7 equidistant points on a circle through the estimated R_{opt} point (Φ-scan). In both scans the targets were presented in random order until each location had been tested 7 times. Other experiments done on the same cells were designed to investigate the neural basis of target selection and relied on experimental paradigms similar to those described by Ottes et al., (1984, 1985). The results obtained in these experiments will be published separately (in preparation).

Eye movements were recorded with the method described by Bour et al., (1984). When adapted for use in monkeys (Van Gisbergen et al., 1985), this method permits a measuring range of about 35 deg in all directions and has an accuracy of 0.25 deg, or better, up to 25 deg eccentricity. The raw eye-movement signals were low-pass filtered (-3 dB at 150 Hz) and digitized with a precision of 12 bits over a range of 100 deg using a 500 Hz sample rate for each signal. The nonlinearity in the raw eye position signals was corrected off line (Bour et al., 1984) based on calibration data from 85 different fixation positions. Saccade detection was performed by a computer program and was subsequently checked by visual inspection of the eye-movement record together with the detected onset and offset moments. Abnormally slow ('sleepy') saccades were rejected by an amplitude (R, in degrees) dependent duration (D, in msec) criterion by requiring that $D < D_{max} = 1.3R + 32$ msec. Trials in which the first saccade was insufficiently precise were excluded from further analysis. We required that saccade amplitude was normometric within 50% and that saccade and target direction agreed within 10 deg. Finally, trials where latency was less than 80 msec, or where fixation of the central spot was less accurate than 1 deg, were also discarded. From the data in accepted trials we determined the mean firing rate of the visual response component in a 100 msec time window starting at stimulus onset and of the movement-related response component from spike data in an identical time window positioned symmetrically around the onset of the first saccade.

RESULTS

Estimation of mapping parameters

We will first discuss results obtained by using the simplest version of our mapping function [$B_u = B_v$, isotropic mapping function, see equations (1) and (2)]. It appears that systematic differences between the collicular representations of upper and lower half of the hemifield in the Cynader and Berman map preclude good fit with our model (Fig. 2A; Table I). As can readily be seen from the quadrant-related differences in the location of comparable points in experimental and theoretical map, the best fit is an ugly compromise which is unsatisfactory for either half of the map.

Since the colliculus is shaped like a bulged roof which slopes laterally and caudally, the fact that Berman and Cynader, unlike Robinson, penetrated in the vertical direction may have caused some distortion if the slanted SC layers were approximated as being horizontal. If this is indeed a contributing factor, it seems least relevant for the medial part of the SC which represents the upper quadrant. Anyway, if the lower-quadrant data are left out the fit with the isotropic mapping model (Fig. 2B, Table I) improves considerably. The mean distance between corresponding points in the experimental and the model map, is now only 100 μm which may well approximate the experimental error in the data base.

Fortunately, a much more extensive set of experimental mapping data is available from Robinson's work. The isotropic version of the mapping function (Fig. 2C; Table I) mimicks the gross features of the motor map quite well (mean error: 240 μm) but the remaining errors are too systematic to be ignored. The most striking shortcoming of the isotropic mapping

model is its underestimation of the size of the collicular map along the v dimension. Indeed, by allowing B_u and B_v to vary independently ('anisotropic mapping function) the fit improves (Fig. 2D, Table I): mean error is reduced from 240 to 190 μm. Still, systematic errors remain. Iso-eccentricity lines for R > 30 deg, for example, are less curved in the anisotropic mapping model than they are in the data. Due to this deficiency of the model, the three datapoints on the minus 60 deg meridian contribute heavily to the sum of squared errors. If these points had been left out, the leftward shift of many model map points relative to the data points would have been less. The optimal parameters for the horizontal meridian alone (B_u = B_v = 1.4 mm/deg; A = 2.7 deg) are strikingly similar to those found for the entire map fit with the anisotropic model. The mean error found in this case is only 30 μm so that the model can match these data almost perfectly. Various types of explanation for the partial discrepancies between model description and experimental data will be delt with later (Discussion).

In our model we have assumed that the afferent and efferent mapping can be regarded as mathematically identical. The obvious way to check the validity of this assumption is to compare the optimal parameters obtained by fitting a given mapping model on visual and motor map data. Unfortunately, the circumstance that the visual map data set is so limited makes such an evaluation premature. In what follows, we retain the assumption of afferent/efferent mapping identity and will use the parameters estimated from the most complete set of data presently available, Robinson's motor map, for describing the fields of collicular neurons. Since we were curious about whether the slightly better fit afforded by the anisotropic mapping model would be reflected in a better fit of field data, we will present results based on either mapping model (isotropic and anisotropic).

Estimation of weighting function parameters from visual and movement field data

We will now illustrate how the model can be applied for the estimation of the best fitting connectivity function (for visual field data) and population activity profile (for movement-field data) if one wishes to interpret electrophysiological data of SC cells in terms of the model's weighting function. As stated above, the mapping function parameters, determined from Robinson's data (Table I), will be used and remain fixed. Unless stated otherwise, we use the simplest mapping function (B_u = B_v = 1.8 mm/deg; A = 5.3 deg) in combination with the circular weighting function [equation (3)]. We call this combination the isotropic model. We are aware that the value of our data, because of the small sample size, is mainly heuristic. Despite its limitations, the data enable us to see better the type of questions invited by the model and gives us a first glimpse of the answers that might be obtained. Before presenting results, we wish to make clear how our fit curves (Figs 3,4) were obtained and how they should be interpreted. In Fig. 3A the saccades made by the monkey when we performed R- and Φ-scans to characterize the movement field of a cell are shown. The variability in the saccades causes both scans to occupy a certain width. The two bold lines in Fig. 3A represent the mean amplitude of the Φ-scan and the mean direction of the R-scan saccades, respectively. After replotting in the model's collicular space (Fig. 3B) the lines become somewhat curved. In the same figure we have also depicted the best-fitting weighting function.

It is helpful now, to add a third dimension to Fig. 3B by imagining that the firing rate associated with each saccade is represented in the height above the page. If this were done, the highest rates would be near, but not necessarily precisely at the center point of the weighting function found by the fitting procedure. The computer varies these parameters as well as its height and its width, until the dome surface fits the firing-rate-representing bars optimally. Thus, fortunately, it is not critical that the R- and Φ-scan passes exactly through R_{opt} and Φ_{opt} of the field. A further point worth considering is that, since the weighting function is circular, the Φ-scan data may require a different width than do the R-scan data. Since the fit is simultaneous in two dimensions, the fitting program will seek a compromise (see below).

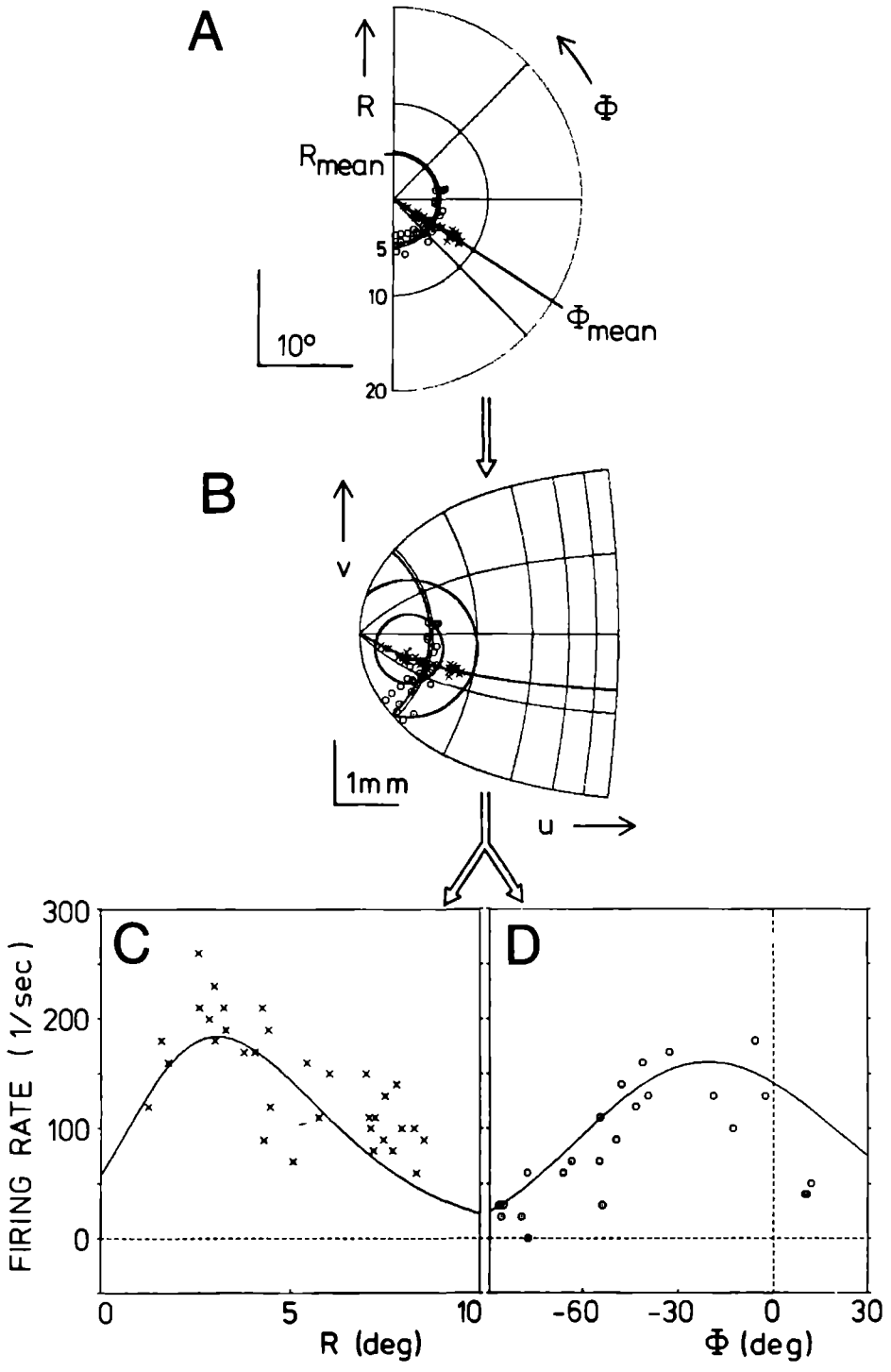

Fig. 3. Parametrization of weighting function.
A. Shows the vector endpoints of saccades made during a Φ-scan (small circles) and an R-scan (crosses) through the movement field of cell 11-21-05. The thick lines represent the mean amplitude of the Φ-scan saccades (R_{mean} = 4.7 deg), and the mean direction of the R-scan saccades (Φ_{mean} = -32.2 deg). For orientation a regular polar-coordinate grid has been superimposed. B. The same saccade endpoints as in A, replotted in collicular coordinates of the isotropic model. In addition, the contour lines at σ and 2σ of the weighting func-

Table II: OPTIMAL PARAMETERS ISOTROPIC MODEL

Cell code	field type	N	R_{opt} (deg)	Φ_{opt} (deg)	u_c (mm)	v_c (mm)	σ (mm)	W_{max} (sp/sec)	error (sp/sec)	goodness fit, r
10-32-01	V	57	1.8	-35	0.5	-0.3	0.17	50	12	0.55
	M	57	1.0	-57	0.2	-0.3	0.25	250	62	0.71
10-42-03	V	56	25	-28	3.1	-0.7	0.35	130	18	0.87
	M	- - -	- - -	- - -	- - -	-not determined	- - -	- - -	- - -	- - -
11-03-03	V	91	10	-35	1.8	-0.7	0.36	340	35	0.91
	M	91	10	-34	1.8	-0.7	0.22	240	18	0.80
11-16-03	V	66	16	-12	2.4	-0.3	0.48	80	12	0.86
	M	66	13	-10	2.2	-0.2	0.61	50	15	0.65
11-17-01	V	61	27	-31	3.2	-0.8	0.44	60	8	0.83
	M	61	24	-38	2.9	-1.0	0.77	410	31	0.95
11-18-04	V	92	9	-16	1.8	-0.3	0.51	100	12	0.86
	M	92	12	-16	2.1	-0.4	0.64	360	42	0.91
11-19-01	V	74	25	-40	3.0	-1.0	0.80	70	12	0.83
	M	- - -	- - -	- - -	- - -	-not determined	- - -	- - -	- - -	- - -
11-21-05	V	- - -	- - -	- - -	- - -	-not determined	- - -	- - -	- - -	- - -
	M	58	3	-22	0.8	-0.2	0.54	190	33	0.74

Table II. Abbreviations: V = visual, M = motor; N is number of trials used in the fit; error = mean absolute difference between calculated and measured firing rate; r = correlation coefficient between calculated and measured firing rates.

The results of the fitting procedure can be evaluated visually by showing the best-fit firing rate as a function of R for the mean saccade direction in the R-scan and as a function of Φ for the mean saccade amplitude in the Φ-scan. Especially when the field is small and the behavioural variability approaches the permitted boundaries (see Methods), the discrepancies between the best-fit line and the actual firing rates (Fig. 3C,D) suggest a poorer fit than was actually obtained (r=0.74). What one would need to show, ideally, instead of two cross-sections through the dome's surface as in Fig. 3C,D, is a 3-D rendering of two relevant slices cut from the spatial weighting function in Fig. 3B. The best-fit results obtained with the isotropic model (see above) for all cells (7 visual fields; 6 movement fields) are summa-

tion, which optimally fits the movement field data of this cell, are shown. By definition [see equation (3)] the weighting function has zero value beyond the projection of the vertical meridian. Note that the R- and Φ-scan represent curved sections through the weighting function. C. Firing rate versus saccade amplitude for the R-scan data, and the corresponding cross section of the optimal weighting function (as in panel B) replotted versus amplitude for $\Phi = \Phi_{mean}$. D. Firing rate versus saccade direction for the Φ-scan data together with the corresponding cross-section of the optimal weighting function (as in panel B) replotted versus direction for $R=R_{mean}$. Note that fit can be improved by using the anisotropic model I (r = 0.85; see Table III),

rized in Table II. The correlation coefficients computed from the actual and best-fit firing rates, for each of the 13 fields, range from 0.71 to 0.95, except in two cases. Another indication of the goodness of fit can be derived from a direct comparison of best-fit curves, defined as explained in the previous section and Fig. 3, with the actual R- and Φ-scan data points (Fig. 4A).

The model curves through the R- and Φ-scan data points (Fig. 4A) fit the movement-field data of unit 11-18-04 (see Table II) quite well ($r = 0.91$), but on closer inspection, the width of the weighting function which is optimal for the combined R- and Φ-scan data does not seem to be the ideal match for either alone. There is a suggestion for both units shown in Figs 3C,D and 4A that the weighting function should be somewhat broader for the R-scan and more narrow for the Φ-scan data. This situation calls for a certain amount of anisotropy, which the isotropic model cannot provide. Hence, it seemed logical to explore two alternative, but closely related, models:

Anisotropic model I :

isotropic mapping function ($B_u = 1.8$, $B_v = 1.8$, $A = 5.3$; see Table I) in combination with an elliptical weighting function [equation (4)].

Anisotropic model II:

anisotropic mapping function ($B_u = 1.4$, $B_v = 1.8$, $A = 3.0$; see Table I) in combina-

Table III: OPTIMAL PARAMETERS ANISOTROPIC MODEL I

cell code	field type	σ_u (mm)	σ_v (mm)	error (sp/sec)	goodness fit, r	σ_u/σ_v
10-32-01	V	0.22±0.05	0.10±0.01	12	0.60	2.2
	M	0.26±0.03	0.20±0.03	54	0.69	1.3
10-42-03	V	0.46±0.11	0.32±0.02	16	0.90	1.4
	M	- - - - - - - - - - - - not determined - - - - - - - -				
11-03-03	V	0.40±0.02	0.34±0.02	35	0.91	1.2
	M	0.40±0.03	0.20±0.01	16	0.82	2.0
11-16-03	V	0.61±0.05	0.40±0.03	10	0.89	1.5
	M	0.75±0.09	0.41±0.04	11	0.79	1.8
11-17-01	V	0.43±0.08	0.44±0.04	8	0.84	1.0
	M	0.96±0.19	0.76±0.04	31	0.95	1.3
11-18-04	V	0.61±0.04	0.41±0.01	11	0.88	1.5
	M	0.74±0.04	0.56±0.02	28	0.95	1.3
11-19-01	V	0.90±0.20	0.73±0.06	12	0.84	1.2
	M	- - - - - - - - - - - - not determined - - - - - - - -				
11-21-05	V	- - - - - - - - - - - - not determined - - - - - - - -				
	M	0.73±0.07	0.38±0.04	24	0.85	1.9
mean	V	0.52	0.39			1.3
	M	0.64	0.42			1.5

Table III. Abbreviations: V = visual, M = motor; σ_u = width of connectivity function along u axis; σ_v = width of connectivity function along v axis; error = mean absolute difference between calculated and measured firing rate; r = correlation coefficient between calculated and measured firing rates.

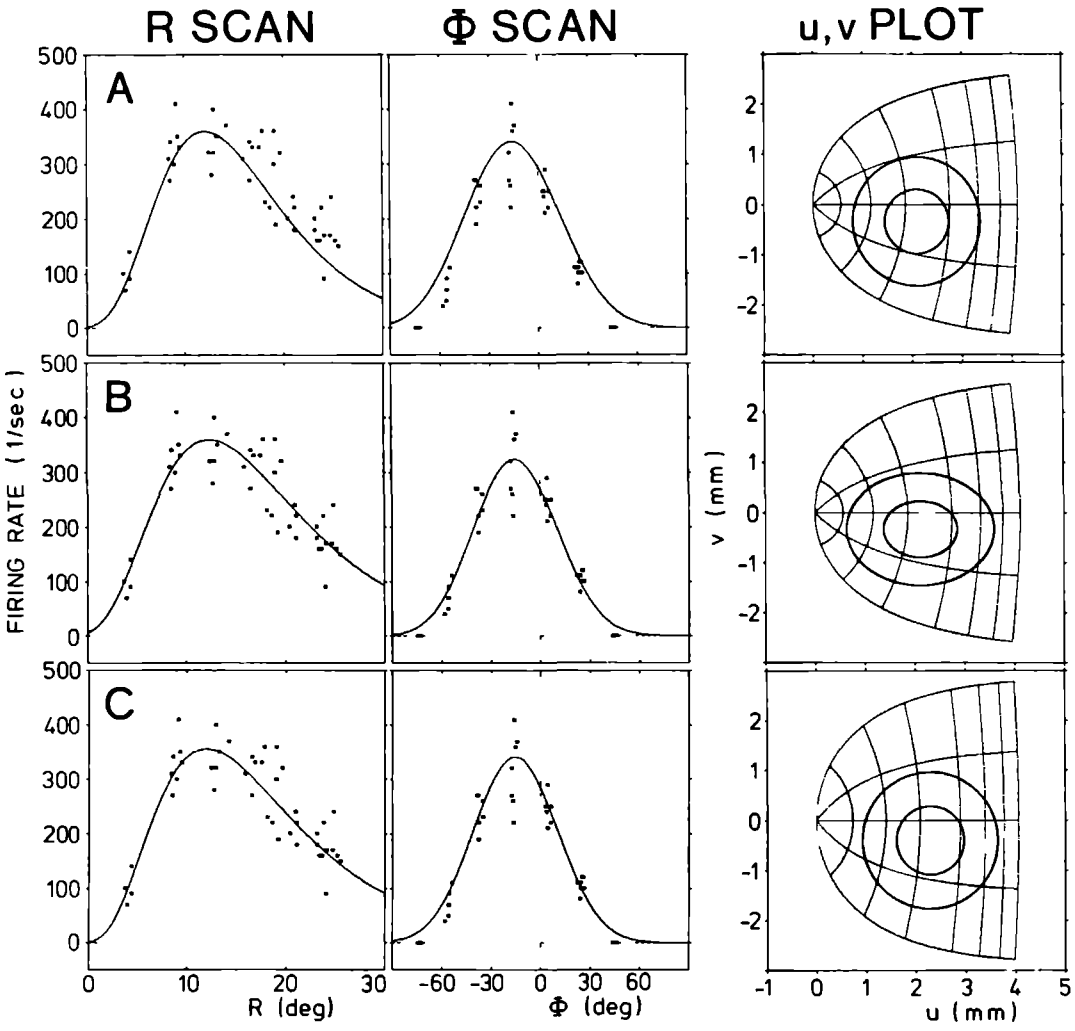

Fig. 4. Best-fit results for R- and Φ-scans through the movement field of an SC neuron, obtained with three different versions of our model. The saccades made in the R-scan (left-hand column) had a mean direction of -17.2 deg, close to the Φ_{opt} value of this cell (see below), and amplitudes ranging from 3.8 to 25.2 deg (horizontal axis). The mean firing rate in the 100 msec time bin around the onset of each saccade (see Methods) is plotted along the vertical axis. The R_{opt} value of this cell (unit 11-18-04) is about 12 deg (see also Table II). The data points in the Φ-scan (middle column) represent the mean firing rate in each individual trial as a function of saccade direction (horizontal axis). The saccades made in this scan had directions ranging between -74.2 and 46.1 deg and a mean amplitude of 14.3 deg, close to the R_{opt} value of the movement field. The Φ_{opt} value of the movement field is about -16 deg (see also Table II). The best-fit curves through the R-scan and Φ-scan data points in the three rows from top to bottom were derived from the three model versions discussed in the text. The right-hand column shows the structure of the collicular map for each model version (thin lines) as well as the σ and 2σ contours of the best-fitting spatial weighting function (heavy lines). The (u_c, v_c) point of the spatial-weighting function is denoted by a dot. The fit lines through the R-scan and Φ-scan data points are in fact sections through the spatial-weighting function in the corresponding panel on the right, replotted in motor space (see text). A. Isotropic model consisting of combination of isotropic-mapping function and circular-weighting function. Goodness of fit: r = 0.91. B. Anisotropic model I, with an elliptical-weighting function and same isotropic-mapping function as in A. Goodness of fit: r = 0.95. C. Anisotropic model II, with anisotropic-mapping function and a circular-weightingfunction, which is different from the weighting function in A, because here it is determined with anisotropic mapping formula. Goodness of fit: r = 0.95.

tion with circular weighting function [equation (3)].

The results of using these two anisotropic models to fit the same data as in Fig. 4A are as expected (Figs 4B,C) inasmuch as the model curves can match the tails of the R- and Φ-scan data better. The right-hand panels in Fig. 4 are helpful in visualizing the main differences among the three versions of our model. The panels show the best-fitting weighting function superimposed on the collicular surface for each model. In both anisotropic models the 2σ contour of the weighting function does not reach the Φ = 45 deg meridian representation (unlike in A), either because the weighting function has shrunk in the v direction (B) or because the Φ = 45 deg meridian representation itself has shifted (anisotropic mapping function, C). It is equally instructive to inspect the position of the 2σ contour relative to the various iso-eccentricity curves in each of the three maps.

The fit provided by anisotropic model II, judged from the difference in correlation coefficients, is significantly better than the isotropic model result, but only by a narrow margin ($p < 0.05$; $z = 1.67$). Because the trial-to-trial variability in firing rate is rather large, the improvements in the other cells, based on the criterion, were not significant. More extensive data sets for each cell would be needed to evaluate the various models more definitely.

The results obtained with anisotropic model I are summarized in Table III where it can be seen that the best-fitting weighting function was elliptical ($\sigma_u \neq \sigma_v$) in 12 out of 13 fields. In all of these fields the anisotropy is in the same direction: the weighting function is elongated in the u-dimension ($\sigma_u > \sigma_u$). The effect seems most pronounced in the case of movement fields (mean $\sigma_u/\sigma_v = 1.5$; see Table III) where it attains the $p < 0.05$ significance level, despite the small sample size (t-test for dependent samples; $t = 2.06$).

Finally, the data in Table II are relevant for testing the prediction from our model that visual fields and movement fields in the same collicular mapping column should have concentric weighting functions (see Introduction). Based on data from five cells where both types of field were determined and fitted, the average offset between their center locations is 0.19 mm, which corresponds with ~11% of the largest field diameter in each individual cell. Field radius was taken as the 2 σ value.

DISCUSSION

Nonhomogeneity of afferent and efferent mapping

It is known that, in addition to retinal inputs, deeper layer SC cells also receive many other inputs, notably from area 17 and the frontal eye fields. Any of these inputs, or a combination of them, may be responsible for the visual and movement field properties of deeper layer cells. In our model (Fig. 1A) the different parallel input channels have been lumped together in a single visual map. This is permissible only if the visual mapping functions in these channels are mathematically similar. We reasoned that lumping is justified, from the standpoint of modeling, as long as the net effect of the various channels can be characterized by similar non-homogeneous mapping functions in combination with a symmetrical spatial weighting function defined on the resulting distorted retinal representation. The interesting and important question to what extent the visual mapping functions in area 17, the frontal eye fields and the SC are actually isomorphic, i.e., different in size but not in shape, cannot be settled at the moment. Some impression can be gleaned by comparing best fit-results obtained with the reasonably satisfactory isotropic model in the SC (Table I) and area 17 (see e.g. Hubel and Freeman, 1977; Van Essen et al., 1984). The value of 5.3 found for A in the collicular map is larger than best fit values reported for area 17 in the monkey which range from 0.3 deg (see Dow et al., 1981) to 1.7 deg (see Tootell et al., 1982). For scaling factor B (subscript irrelevant here because $B_u = B_v$) we found 1.8 mm/deg in the SC (Table I). Since area 17 is so much larger, its B values are much higher (8.6 to 15.7 mm/deg; see: Dow et al., 1981; Tootell et al., 1982). The frontal eye field map is not known in detail but Bruce and Goldberg's results show that nonhomogeneous mapping is probably an important mechanism underlying the spatial properties of

visual and movement fields of its neurons. Thus, in summary, nonhomogeneous transformation of the visual field seems a common property of both the retinal and the indirect visual inputs to the superior colliculus. Although a quantitative assessment is not yet possible, the resulting distortion seems qualitatively similar in each input (cf. McIlwain, 1977).

Following this discussion on whether the visual mappings in the various parallel inputs are isomorphic, it is equally pertinent to ask whether the afferent and efferent mapping are really isomorphic as we supposed (Fig. 1A,B). As will have become clear from the Results (see Fig 2 and Table I), the visual map data available are too scant to reach a firm conclusion. In case the upper/lower quadrant asymmetry in the Cynader and Berman data is real (see Results) the assumption of afferent/efferent mapping isomorphism seems untenable. Another hint in the same direction is the fact that the oculomotor range is more limited than the visual field. This means that isomorphism must at least be violated in the extreme periphery.

It should be pointed out that, so far, motor map data are absent for nearly vertical saccades. It has been argued that the generation of these saccades may require signals in both colliculi (Robinson, 1972), a situation which cannot be mimicked with a single stimulation electrode. To what extent this may have caused some distortion already for the oblique saccades in Figs 2C,D cannot be ascertained. The circumstance that the collicular map is embodied in a curved cell layer, adds another complication which may have been responsible for some additional distortion in the experimental two-dimensional map. In view of these uncertainties, we have retained the isomorphism assumption. The afferent and efferent mapping functions can be made different if the need arises but, of course, a balance must be maintained between the conflicting desires for increasing the precision of the model and for retaining its lucidity.

Saccade-related activity in the SC and its transformation to movement

In our model the population activity of a group of cells centered around a certain SC mapping column is transformed into a saccade which moves the eye to the corresponding external world point (see Fig. 1A and Introduction). This description of the relation between intrinsic neural activity in the SC and the metrics of the resulting eye movement was sufficiently precise to serve as our definition for the efferent mapping function, but says nothing on underlying neural mechanisms. The efferent mapping is merely an abstract description of the total effect of signal processing which must intervene at various levels to transform collicular neural activity, ultimately, into movement. How this transformation is realized at the single neuron level downstream of the SC is still a problem for future electrophysiological work. For a further discussion on this topic we refer to Van Gisbergen et al. (1985).

Because of the present lack of relevant neurophysiological data, we must content ourselves now with discussing possible mechanisms on a more abstract level. McIlwain (1982) and Sparks et al. (1976) have offered interesting suggestions on how the activity in a large population of active SC movement-related cells could bring about a goal-directed eye movement. They proposed to consider the saccade as the total sum of many miniature movement vectors, each caused by the activity of a single SC cell. In what follows, we will elaborate their basic idea.

We adopt the miniature vector idea sketched above, but like to stress first that we regard each miniature vector as a position or error signal signifying a desired displacement. This seems justified because SC neurons carry no information on eye velocity (Sparks and Mays, 1980). The transformation from the SC position signal into an eye velocity signal must occur downstream, in the brain stem (Hepp and Henn, 1983; Van Gisbergen et al., 1985).

Suppose that each active cell in the pool of SC movement cells codes its own miniature desired-displacement vector (minivector, for short) whose direction (ϕ) is identical with the Φ_{opt} value of that particular neuron:

$$\phi(u,v) = \Phi_{opt}(u,v) \qquad (5)$$

A comparable suggestion was made by Georgopoulos et al. (1983, 1984) in their discussion on the possible role of motor-cortex neurons in the control of two-dimensional arm movements.

The relation between collicular location and Φ_{opt} has not been measured in its entirety, but since Schiller and Stryker (1972) have demonstrated that the saccade direction (Φ) evoked by electrical stimulation at a collicular site (u,v) is roughly equal to $\Phi_{opt}(u,v)$, the direction of each cell's minivector can be estimated from Robinson's (1972) motor map. Alternatively, if one is willing to ignore its imperfections, the mathematical mapping function can be used to compute the minivector ϕ-value at any collicular location (see Appendix II and Fig. 2D).

Now suppose, in addition, that the amplitude (r) of each minivector is determined by

$$r(u,v) = M(u,v) \cdot W(u-u_c, v-v_c) \qquad (6)$$

where W is the firing rate of the local cell, depending on the distance between its position (u,v) and (u_c,v_c) [cf. equation (3) or (4)]. The function M(u,v) is a local gain factor, which, since r is expressed in degrees and W in spikes/sec, has the dimension of deg/(spikes/sec). Of course for neurons representing large eccentricities, M would be larger than for small-eccentricity neurons (Sparks and Mays, 1981).

For the idea expressed in equations (5) and (6) to be viable, the vector sum of all these local minivectors, generated by the total population of cells, must be the desired saccade which is needed to bring the eye on target. The general idea expressed by McIlwain and Sparks et al. can be incorporated in our model if it is possible to find a fixed function M(u,v) [see equation (6)] which specifies the gain factor for converting firing rate into amplitude of movement at each collicular site. Finding out whether such a fixed set of collicular gain factors can exist within the constraints of our model, is a clearly defined but nontrivial problem which will require more work. At present, we see no a priori reasons why this should not be possible. There is one final point to be made in this context. Since each cell in the population of recruited SC cells is thought to contribute to the saccade, the total effect of the population activity will depend on how many cells are active. This necessitates some kind of normalization to ensure that the total sum of all contributions is a normometric saccade. If the population activity profile is invariant throughout the colliculus as we assumed (see Introduction) no additional normalization is needed in our model.

Quantitative models have been a powerful challenge for experimentation in the peripheral oculomotor system [for a review, see Robinson (1981)]. These models have allowed neurophysiologists to confront single unit data with model predictions and have led to simulations of normal and abnormal saccades (Van Gisbergen et al., 1981; Zee and Robinson, 1979).

We regard the scheme presented in this paper as a first step in the development of a quantitative comprehensive model of the oculomotor system which incorporates collicular signal processing. Concepts such as the mapping function and the spatial weighting function are likely to survive in some form as essential elements in a more complete model. So far, our model is too incomplete to have real predictive power. Its present purpose is to serve as a framework for the quantitative description of single-cell properties. Parametrization of cell properties in terms of the model makes it possible to characterize each cell in a functionally meaningful way with just a few numbers. This is especially welcome in the study of visuomotor neurons whose asymmetric visual and movement fields, at first sight, may seem to make quantitative description a hopeless undertaking.

If a more mechanistically oriented scheme along the lines sketched above [equations (5) and (6)] could replace the purely descriptive mapping function without affecting the overall input-output relationship, our model could be used for simulations, e.g., to predict the effect of local SC lesions. This is such a recurrent theme in discussions in the literature that a quantitative model seems badly needed. Such a more complete model could also be used to investigate the effect of collicular noise on the precision of visually guided saccades. If the scheme in Fig. 1A is valid, collicular noise would be expected to have its most disruptive effect, in terms of absolute error, in large saccades. When expressed in a relative measure, the inaccuracy might be expected to be more or less constant over the full oculomotor

range. In this case, the argument could be reversed: if constant relative precision can be regarded as a desirable property in the saccadic system, the pronounced nonuniformity of collicular maps may have a functional meaning.

Deficiences in the present model

Our scheme is very incomplete in modeling the activity of visual cells in the upper layers. The dependence of the response of these cells on stimulus intensity and contrast and the presence of surround and nonlinear response mechanisms has been glossed over. In its present state the scheme can only give an impression of the activity in the visual map created by a point stimulus.

Another deficiency is that the model does not describe how visual activity in the upper SC layers, or in other sources, is converted into movement-related activity. Why do two visual stimuli evoke a compromise response when closely spaced (Findlay, 1982), and a saccade to one or the other target when sufficiently wide apart (Ottes et al., 1984, 1985)? One way to investigate this target selection process would be to determine whether the movement fields of SC neurons are different for single versus double-stimulus responses.

A perhaps more fundamental shortcoming of the model is its failure to account for the variation in visual field and movement field sizes in each collicular mapping column. How essential it is to incorporate this variability in the model is difficult to assess as long as it is not known which of these cells have connections with the motor system.

Finally, we did not specify how the model could be applied on movement fields not contained within one half field (Sparks et al., 1976). The formulas (1) and (2), in our present model, transform the right half of the field of view (or the oculomotor space) onto one colliculus. A similar set of equations would transform the left half onto the other colliculus. As long as visuomotor fields are situated in one half of the external space, i.e. do not transgress the vertical axis, they can be approximated within one collicular map using a contiguous weighting function. This procedure cannot be applied in a straightforward manner on movement fields which do cross the vertical axis. It would be a logical extension of our model in line with ideas expressed in the literature (Robinson, 1972) to assume that such movement fields reflect two clusters of active cells along the vertical meridian representation, one in each colliculus. The simplest possibility to be tested for such cells, would be to fit the part of the movement field contained in each half field separately with a Gaussian weighting function, zero valued beyond the collicular boundary [see equation (3)], in each corresponding colliculus. The precise consequences of this idea for the minivector hypothesis, outlined above, remain to be worked out.

Appendix I: Reciprocity between the connectivity function of one neuron and the population-activity in response to a point stimulus in the model.

Consider a one-dimensional section of the collicular map representing e.g. the horizontal axis of the visual field. Let $W(u_i,u_j)$ describe for any neuron i (i=1,...,N) at location u_i its connectivity with any axon j (j=1,...,M) entering the colliculus section at location u_j.

The firing rate F of a particular SC neuron I, located at position u_I, may then be expressed as:

$$F_I = \sum_{j=1}^{M} W(u_I,u_j)R_j \qquad (A1)$$

where R_j is the activity of axon j.

The connectivity function C in our model is determined by how an axon j contributes to the firing rate of a particular SC cell I at position u_I, depending on the axon's position u_j:

$$C_I(u_j) = W(u_I,u_j)\, R_j \quad j = 1,...,M \qquad (A2)$$

The profile of the population of active neurons, caused by the activity R_j in a particular axon J, in turn due to a visual point stimulus, can be represented as the function:

$$P_j(u_i) = W(u_i,u_j)\, R_j \quad i = 1,...,N \qquad (A3)$$

Although the connectivity function C and the population profile P are essentially defined on a discrete set of u values, these functions are considered here as being continuous.

We assume in the model that W, instead of a function of two independent variables: u_1 and and u_J, is actually a function of only one variable, the distance d between the locations of the neuron and the axon. Thus, in equation (A2) as well as in equation (A3), the connectivity W can be written as depending on d: W(d). If we further assume that the response to a visual point stimulus is the same in all axons, which is equivalent with $R_J = R$ for $J = 1,...,J,...M$, it follows that the right hand sides of (A2) and (A3) are the same and thus that connectivity function C and population profile P are identical functions of distance d between axon and neuron.

Appendix II: While equations (1) and (2) give the mapping from an external world point (R,Φ) to the corresponding (u,v) point on the collicular map, it is also possible to express the inverse mapping relationship:

$$R = \sqrt{\exp(\frac{2u'}{\beta_u}) - 2A\cdot\exp(\frac{u'}{\beta_u})\cdot\cos(\frac{v}{\beta_v}) + A^2} \quad (A4)$$

$$\Phi = \operatorname{atan} \frac{\exp(\frac{u'}{\beta_u})\cdot\sin(\frac{v}{\beta_v})}{\exp(\frac{u'}{\beta_u})\cdot\cos(\frac{v}{\beta_v}) - A} \quad (A5)$$

where $u' = u + \beta_u \ln A$.

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REFERENCES

Bour L.J., Van Gisbergen J.A.M., Bruijns J. and Ottes F.P. (1984) The double magnetic induction method for measuring eye movement - Results in monkey and man. IEEE Trans. Biomed. Eng. BME-31, 419-427

Bruce C.J. and Goldberg M.E. (1985) Primate frontal eye fields: I. Single neurons discharging before saccades. J. Neurophysiol. 53, 603-635

Capuano U. and McIlwain J.T. (1981) Reciprocity of receptive field images and point images in the superior colliculus of the cat. J. Comp. Neurology 196, 13-23

Cynader M. and Berman N. (1972) Receptive-field organization of monkey superior colliculus. J. Neurophysiol. 35, 187-201

Daniel P.M. and Whitteridge D. (1961) The representation of the visual field on the cerebral cortex in monkeys. J. Physiol. 159, 203-221

Dow B.M., Snyder A.Z., Vautin R.G. and Bauer R. (1981) Magnification factor and receptive field size in foveal striate cortex of the monkey. Exp. Brain Res. 44, 213-228

Findlay J.M. (1982) Global visual processing for saccadic eye movements. Vision Res. 22, 1033-1045

Fischer B. (1973) Overlap of receptive field centers and representation of the visual field in the cat's optic tract. Vision Res. 13, 2113-2120

Friendlich A.R. (1973) Primate head restrainer using a nonsurgical technique. J. Appl. Physiol. 35, 934-935

Georgopoulos A.P., Caminiti R., Kalaska J.F. and Massey J.T. (1983) Spatial coding of movement: A hypothesis concerning the coding of movement direction by motor cortical populations. Exp. Brain Res. Suppl. 7, 327-336

Georgopoulos A.P., Kalaska J.F., Crutcher M.D., Caminiti R. and Massey J.T. (1984) The representation of movement direction in the motor cortex: single cell and population studies. In: Dynamic Aspects of Neocortical Function, pp 501-524 (Edited by: Edelman G.M., Gall W.E. and Cowan W.M.) Wiley, New York

Hepp K. and Henn V. (1983) Spatio-temporal recoding of rapid eye movement signals in the monkey paramedian pontine reticular formation (PPRF). Exp. Brain Res. 52, 105-120

Hubel D.H. and Freeman D.C. (1977) Projection into the visual field of ocular dominance columns in macaque monkey. Brain Res. 122, 336-343

Judge S.J., Richmond B.J. and Chu F.C. (1980) Implantation of magnetic search coils for measurement of eye position: An improved method. Vision Res. 20, 535-538

McIlwain J.T. (1975) Visual receptive fields and their images in superior colliculus of the cat. J. Neurophysiol. 38, 219-230

McIlwain J.T. (1976) Large receptive fields and spatial transformations in the visual system. In: Neurophysiol. II, volume 10, pp 223-248. (Edited by Porter R.) Univ. Park Press, Baltimore

McIlwain J.T. (1977) Topographic organization and convergence in corticotectal projections from areas 17, 18, and 19 in the cat. J. Neurophysiol. 40, 189-198

McIlwain J.T. (1982) Lateral spread of neural excitation during microstimulation in intermediate gray layer of cat's superior colliculus. J. Neurophysiol. 47, 167-178

Mohler C.W. and Wurtz R.H. (1976) Organization of monkey superior colliculus: Intermediate layer cells discharging before eye movements. J. Neurophysiol. 39, 722-744

Mooney R.D., Klein B.G., Jacquin M.F. and Rhoades R.W. (1984) Dendrites of deep layer, somatosensory superior collicular neurons extend into the superficial laminae. Brain Res. 324, 361-365

Ottes F.P., Van Gisbergen J.A.M. and Eggermont J.J. (1984) Metrics of saccade responses to visual double stimuli: Two different modes. Vision Res. 24, 1169-1179

Ottes F.P., Van Gisbergen J.A.M. and Eggermont J.J. (1985) Latency dependence of colour-

based target versus nontarget discrimination by the saccadic system, Vision Res. 25, 849-862

Perry V.H. and Cowey A. 1984) Retinal ganglion cells that project to the superior colliculus and pretectum in the macaque monkey. Neuroscience 12, 1125-1137.

Robinson D.A. (1972) Eye movements evoked by collicular stimulation in the alert monkey. Vision Res. 12, 1795-1808

Robinson D.A. (1981) The use of control systems analysis in the neurophysiology of eye movements. Ann. Rev. Neurosci. 4, 463-503

Schiller P.H. and Koerner F. (1971) Discharge characteristics of single units in superior colliculus of the alert rhesus monkey. J. Neurophysiol. 34, 920-936

Schiller P.H. and Stryker M. (1972) Single-unit recording and stimulation in superior colliculus of the alert rhesus monkey. J. Neurophysiol. 35, 915-924

Schwartz E.L. (1980) Computational anatomy and functional architecture of striate cortex: A spatial mapping approach to perceptual coding. Vision Res. 20, 645-669

Schwartz E.L. (1984) Anatomical and physiological correlates of visual computation from striate to infero-temporal cortex. IEEE Trans. Systems, Man and Cybern. SMC-14, 257-271

Sparks D.L., Holland R. and Guthrie B.L. (1976) Size and distribution of movement fields in the monkey superior colliculus. Brain Res. 113, 21-34

Sparks D.L. (1978) Functional properties of neurons in the monkey superior colliculus: Coupling of neuronal activity and saccade onset. Brain Res. 156, 1-16

Sparks D.L. and Mays L.E. (1980) Movement fields of saccade-related burst neurons in the monkey superior colliculus. Brain Res. 190, 39-50

Sparks D.L. and Mays L.E. (1981) The role of the monkey superior colliculus in the control of saccadic eye movements: A current perspective. In Progress in oculomotor research, pp 137-144.(Edited by Fuchs A.F. and Becker W.) Elsevier North Holland., Amsterdam

Tootell R.B.H.. Silverman M.S., Switkes E. and De Valois R.L. (1982) Deoxyglucose analysis of retinotopic organization in primate striate cortex. Science 218, 902-904

Van Essen D.C., Newsome W.T. and Maunsell J.H.R. (1984) The visual field representation in striate cortex of the macaque monkey: Asymmetries, anisotropies, and individual variability. Vision Res. 24, 429-448

Van Gisbergen J.A.M., Robinson D.A. and Gielen S. (1981) A quantitative analysis of generation of saccadic eye movements by burst neurons. J. Neurophysiol. 45, 417-442

Van Gisbergen J.A.M., Van Opstal A.J. and Schoenmakers J.J.M. (1985) Experimental test of two models for the generation of oblique saccades. Exp. Brain Res. 57, 321-336

Wurtz R.H. and Goldberg M.E. (1972) Activity of superior colliculus in behaving monkey. III. Cells discharging before eye movements. J. Neurophysiol. 35, 575-586

Zee D.S. and Robinson D.A.(1979) A hypothetical explanation of saccadic oscillations. Ann. Neurol. 5, 405-414

COLLICULAR INVOLVEMENT IN A SACCADIC COLOUR DISCRIMINATION TASK

SUMMARY

We have recorded the neural activity of single superior colliculus (SC) neurons in monkeys engaged in a saccadic target/nontarget discrimination task based on a colour cue. Since there are reasons to assume that correct execution of this task depends on cortical signal processing (Ottes et al., 1985), our experiments are of interest for getting a better insight in the problem of how cortical and subcortical signals, relevant in the visual guidance of saccades, are combined. The experiments were designed to distinguish between two extreme possibilities:

1) The crucial cortical signal affects the saccadic system at or above the level of the SC movement-related cells (serial hypothesis) or, alternatively,
2) The colour information bypasses the motor colliculus and affects the saccadic system at a level more downstream (parallel hypothesis).

The saccade-related activity in SC visuomotor neurons, under conditions where the saccadic system had to select the green target stimulus and to ignore the red nontarget spot, remained as tightly coupled to the metrics of the saccade as it was in a simple saccadic single spot detection task. Since these cells, at the time when the saccade was made, thus appeared as able to make the colour discrimination as the total system, we conclude that our data corroborate the serial hypothesis.

The initial sensory burst and the prelude of activity, which occurs some time before the saccade response, appeared to be colour non opponent in all neurons. In some neurons, however, these components in the neural activity were quantitatively slightly different for the green target and the red nontarget. Since these minor differences were colour rather than motor response dependent, they were probably not part of the target selection process. In a few cells the prelude activity depended on response occurrence and response metrics, but only to a rather limited extent.

These data suggest the possibility that the decision as to what saccade should be made (if any) was to a large extent imposed upon the SC visuomotor cells by an external source. These cells, representing the outcome of this process in their saccadic activity, seem to receive the decision information at a very late stage, just before the saccade actually starts. A possible origin of this putative intervening signal is discussed.

Key words: saccadic system; target selection; colour discrimination; superior colliculus; single-unit recording; rhesus monkey

INTRODUCTION

It is well established that the superior colliculus (SC) in the monkey is involved in the generation of visually guided saccadic eye movements. The evidence, on which this concept is based, has been discussed in several recent reviews (Wurtz and Albano, 1980; Sparks and Mays, 1981; Fuchs et al., 1985). In its deeper layers the SC contains neurons which show a movement-related discharge (Wurtz and Goldberg, 1972a; Sparks et al., 1976) before saccades within the movement field of the cell. Cells in these layers have anatomical connections with the reticular formation in the brainstem (Harting, 1977) which contains saccadic burst cells (Luschei and Fuchs, 1972; Keller, 1974; Van Gisbergen et al., 1981) generally held responsible for generating saccades. Local electrical stimulation in the SC at low current strengths gives rise to a saccade (Robinson, 1972) which is directed at the external world point represented by nearby neurons (Schiller and Stryker, 1972). Furthermore, lesions of the SC cause a clear prolongation of latency in contralateral saccades together with a decrease in response precision (Wurtz and Goldberg, 1972b; Schiller et al., 1980; Albano et al., 1982). Local application of substances interfering with GABA-ergic neural transmission causes clear effects on the execution of saccadic eye movements (Hikosaka and Wurtz, 1985a).

On the other hand, it is equally clear that the SC is not the only area involved in generating visually guided saccades. There is now compelling evidence that the frontal eye fields contain movement cells that become active just prior and during purposive and visually guided saccades (Bruce and Goldberg, 1985). Electrical stimulation in the frontal eye fields causes saccadic eye movements (Robinson and Fuchs, 1969). Recent experiments by Bruce et al. (1985) have revealed, in addition, that the metrics of saccades which can be generated at low current strengths are related to the movement-field location of nearby presaccadic neurons. The frontal eye fields have direct connections with intermediate layers in the SC (Leichnetz et al., 1981) as well as with regions in the brainstem reticular formation (Leichnetz et al., 1984; Schnyder et al., 1985). The frontal eye fields may also influence colliculus activity indirectly by modifying the activity of the substantia nigra, pars reticulata, which probably exerts a tonic inhibition on saccade-related cells in the SC (Hikosaka and Wurtz, 1983a,b).

There are some indications that the frontal eye fields and the SC play functionally different roles. For example, the frontal eye fields do not seem to be involved in the generation of spontaneous saccades (Bruce and Goldberg, 1985). By contrast, ablation of the SC reduces the frequency of spontaneous saccades in the affected half field (Albano et al., 1982). In addition, there is preliminary evidence (Sandell et al., 1984) that the SC - but not the frontal eye fields - must be intact for the generation of extremely short-latency saccades (express saccades) first described by Fischer and Bock, (1983). Finally, studies of patients are in line with the idea that the frontal eye fields may be important for executing saccades under conditions where a deliberate strategy is required and reflexive responses have to be avoided (Guitton et al., 1985).

Since there are at least two regions involved in the generation of visually guided saccades, an obvious question of interest is how their signals are combined. The fact that both regions have direct connections with the reticular formation in the brainstem suggests the possibility that the signals may converge at this level. Some indirect support for this idea comes from electrical stimulation experiments by Schiller and coworkers. Schiller et al. (1979) found that combined electrical stimulation in the frontal eye fields and the SC caused a compromise response which was intermediate between the result of stimulating each site separately. Since it had been shown earlier (Schiller, 1977) that electrical stimulation of the frontal eye field, on the side of the brain where the SC had been ablated before, could still elicit saccadic eye movements, Schiller et al. suggested that the compromise response after combined stimulation may reflect convergence of signals at the level of the brainstem saccade generator.

There are also some findings which rather indicate the possibility that SC movement cells are perhaps part of a final common pathway for all saccades. First, Sparks and Porter (1983) have shown that when electrical stimulation in the SC interferes with the execution of a visually elicited saccade, collicular movement cells participate in the generation of a subsequent corrective saccade although the visual target is no longer present. Second, collicular movement cells are also active prior to the generation of saccades to auditory targets (Jay and Sparks, 1984).

In order to learn more on how cortical and subcortical signals important for the guidance of visually elicited saccades are combined we have designed a new paradigm (Ottes et al., 1985) which probably forced the monkey to use cortical signal processing (see below). While the monkey was performing a saccadic target/nontarget discrimination task where a saccade must be made to a green target and a red nontarget stimulus must be ignored, we recorded the activity of a single SC neuron. Target and nontarget stimuli were matched in brightness, size and shape.

In our experiments the monkeys performed the target/nontarget discrimination task quite well (see Results). If they did this by relying on colour discrimination; i.e., by using the most obvious cue available, signals from the geniculostriate colour opponent system must influence the generation of saccadic motor command signals. As far as the involvement of the

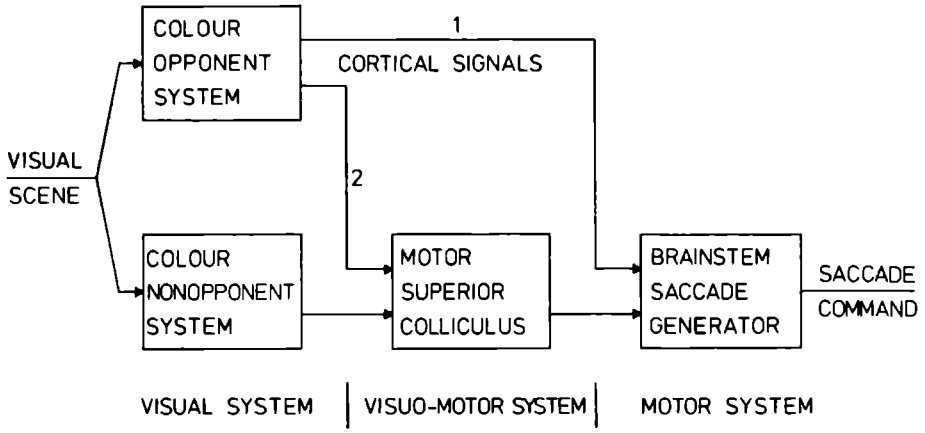

Fig. 1. Black-box diagram of saccadic system to explain logic of the experiment. Movement-related neurons in the deeper layers (box motor superior colliculus) receive colour nonopponent visual information (see Introduction and Results section). This information may come from various sources such as the SC superficial layers and area 17 (see Discussion). These signals may serve to detect target and nontarget stimuli, but are insufficient to identify them. The experiments were designed to test whether the colour information, needed by the saccadic system in order to avoid errors, passes through the SC (2) or reaches the saccadic system downstream of the SC (1). In the Discussion several possibilities for pathway 2, suggested by data from the literature, will be reviewed.

SC is concerned, two extreme possibilities are worth considering (see Fig. 1):

1) The colour-opponent signals relevant here bypass the SC entirely and influence the saccadic system at the level of the brainstem saccade generator. The pathway from the frontal eye fields to the reticular formation (see above) might carry this information.

2) The crucial colour-opponent signals influence the saccadic system upstream or at the level of the SC, e.g. in the frontal eye fields (see Discussion for other possible sources). Before our experiments were done, there was little evidence to support this view. It is known that colour-opponent retinal ganglion cells do not project to the SC (Schiller and Malpeli, 1977). There is no evidence for more indirect routes to the SC either. In a study in anesthetized and paralyzed monkeys, Marocco and Li (1977) found no colour-opponent activity in the SC. Thus, so far, there are no indications that SC visual neurons have access to signals which are deemed crucial in our task.

If the colour-opponent signals bypass the SC (parallel arrangement; pathway 1 in Fig. 1) one would not expect to find, in collicular movements cells, the same tight relation between saccade-related activity and saccade metrics for our double-stimulus discrimination task as for a classical single target task which requires only signal detection. On the other hand, finding the same burst-activity/saccade relationship in both conditions would be in line with a serial arrangement of the colour-opponent system and the SC (pathway 2 in Fig. 1). Our results from SC visuomotor cells support the serial arrangement hypothesis.

METHODS

Two male rhesus monkeys were trained to refixate a green spot of light after it jumped from a central fixated position to a peripheral

position. The animals, which had been water deprived for up to 16 hours, were rewarded with apple juice when on target. The monkeys underwent three separate operations (halothane-nitrous oxide anesthesia) under aseptic conditions:

1. A crown, modified after Friendlich (1973), was attached to the skull with dental cement and medical bone screws (Synthes). The crown served to stabilize the head during the experiments and to accept the pick-up coil for measuring eye movements with the double magnetic induction method (see below).
2. A gold-plated thin copper ring was implanted beneath the conjunctiva on the right eye using the surgical technique described by Judge et al. (1980). This ring was used to record eye movements with the double magnetic induction method (see below).
3. A closed stainless-steel chamber, its axis oriented at a point between the two superior colliculi, was implanted stereotaxically over a hole trephined in the skull. During each operation the animal was artifically respirated and end-tidal CO_2, heart rate and body temperature were continuously monitored.

During electrophysiological experiments a coated tungsten microelectrode (Bak Inc.) having an impedance of 0.8-1.5 MΩ at 1 kHz, was lowered inside a guide tube through the dura. The micro-electrode signal was amplified (Grass P16 pre-amplifier) and monitored on a storage oscilloscope. Action potentials of isolated units were discriminated from background noise by level detection. Their moments of occurrence, timed with a precision of 0.1 msec, were stored in the computer. As the electrode was lowered slowly under hydraulic control, visual stimuli were presented on the screen while the monkey was kept alert. The point of entry into the superficial layers of the SC was taken as the electrode position where visually driven background activity was first noticed unmistakably. When action potentials from a single neuron were isolated, a more systematic search for its visuomotor field began. Visual stimuli were rear projected on the large translucent screen which had a background luminance of 1.2 cd/m^2 and was placed at 57 cm from the monkey. The round green target spot had a diameter of either 0.4, 0.9 or 2.0 deg and a luminance of about 5 cd/m^2. The larger diameter stimuli were used for visuomotor fields at larger eccentricity (0.9 deg beyond 10-15 deg; 2.0 deg beyond 20-25 deg). Vision was binocular. To locate the field of a neuron, the target was presented in a random sequence at each of 49 positions in a relevant sector of the visual field (field-scan). In this sector, 7 eccentricities were tested at each of 7 meridional angles. The range of the field scan could be adapted independently in the R and the Φ direction to fit the need for any particular cell. Each trial of the field scan started with the presentation of the target at the primary position during 0.8 to 1.8 sec. Then the central spot was switched off, and after the screen was blank for 12 msec, the target reappeared at one of the 49 positions. At each peripheral position, the spot remained stationary for 2 sec until it was extinguished and the intertrial pause (duration 1-2 sec) began. To investigate the field further, stimulus sequences could then be run which were limited to 7 equidistant positions along a meridian through the estimated most responsive field location (R-scan) or to 7 equidistant points on a circle through this point (Φ-scan). In both scans the target was presented in random order until each location had been tested 7 times. In a small number of units, a repetitive stimulus was presented, after the scans were completed, where the peripheral position was always at the center of the field. In these experiments timing was the same as in the scan sequences. The results obtained with these stimulus scans have been described elsewhere (Ottes et al. 1986).

In the next series of trials, which formed the main goal of the present experiments, the monkey was confronted with equally sized and shaped red (Wratten filter 25) and green (Wratten filter 58) round spots of light which, to the experimenters, appeared matched in brightness. The size of the stimuli was always chosen large enough so that the monkey could do most of trials correctly. In these experiments stimuli were either presented in the visuomotor field of the neuron (field stimuli), along a meridian opposite the field (anti-field stimuli), or at the fixation point in the primary position. In the earlier experiments the so-

called anti-field stimuli had an eccentricity of 0.5, 1.0 or 1.5 times the eccentricity of the field stimuli. Later on, field and anti-field stimuli were at the same eccentricity.

Each trial began with a green fixation stimulus at the primary position which remained on for 0.5 to 1.5 sec (scene 1). After a blank period lasting 12 msec one of the various

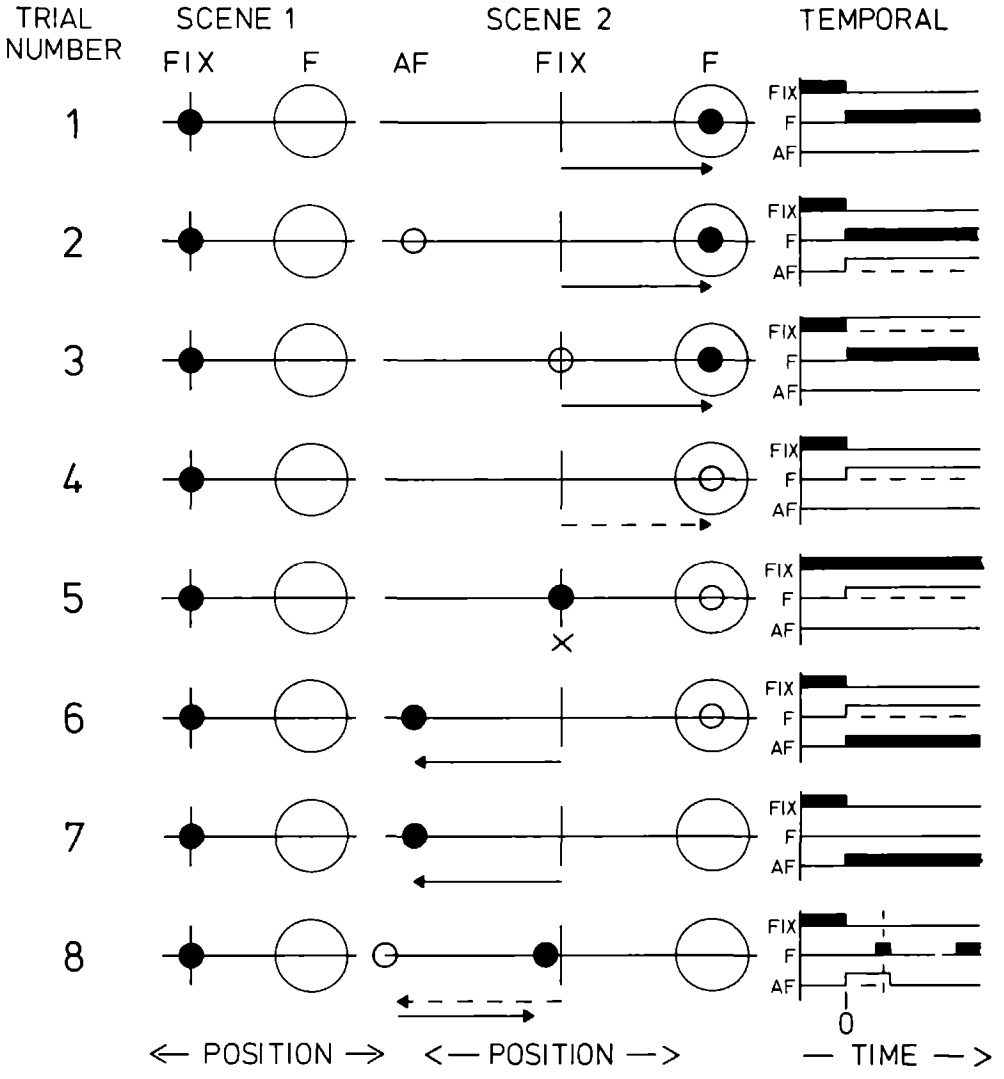

Fig. 2. Diagram of trial types. Each trial began with the target stimulus at the primary position (scene 1; left hand column) and was followed by one of the 8 different stimulus patterns described in the text (scene 2; middle column). The target and the nontarget spot are denoted by a closed and an open small circle, respectively. The arrows in the middle column show the direction and the size of the saccade the monkey was expected to make. Saccades indicated by dashes lines (to the nontarget stimulus) were not rewarded. The cross, instead of an arrow, in scene 2 of trial 5 indicates that in this case the expected response here is a continuing fixation. The large circle superimposed on each scene denotes the contour of a schematic receptive field. The closed bars (target stimulus on) and the open bars (nontarget stimulus on) in the right-hand column show the temporal relations (not to scale). Trial type 8 consisted in fact of a series of different scenes. The second scene shown is taken at the moment indicated by the dashed vertical line in the temporal relations diagram on the right. Shortly after this scene both stimuli were off. One second later the fixation spot reappeared at the central position. Abbreviations: FIX = fixation position; F = field position; AF = antifield position.

scenes depicted in Fig. 2 appeared (scene 2). When the sequence was run to completion, the total number of trials was 72 or 110 for the two different sequences which have been in use. The stimuli lasted for 1-2 sec, and are listed below. Presentation was in a random order.

trial type 1 The green target spot appears in the visuomotor field (6 or 10 trials). The monkey is required to make a field saccade (arrow in Fig. 2) in order to obtain reward.

trial type 2 The green spot is presented at the visuomotor field while the red nontarget stimulus is presented simultaneously at the antifield position (18 or 20 trials). The monkey is rewarded for making a field saccade.

trial type 3 The green target spot is presented in the visuomotor field with the nontarget stimulus at the primary position (6 or 10 trials). The monkey is required to make a field saccade.

trial type 4 After the green fixation spot extinguishes, the red nontarget spot appears in the visuomotor field (catch trials; 6 or 10 trials). Although fixation of the red spot was never rewarded, this enticing stimulus in fact often evoked a saccade.

trial type 5 The red spot of light is presented in the visuomotor field while the green spot remains at the primary position (6 or 10 trials). This trial, where the monkey should maintain central fixation, provides an opportunity to measure the neural activity when a visual stimulus in the neuron's visuomotor field is being ignored by the monkey. The remaining response in this case must reflect passive sensory properties of the neuron.

trial type 6 The green spot is presented at the antifield position simultaneously with the nontarget stimulus in the visuomotor field (18 or 30 trials). The monkey is required to make an antifield saccade.

trial type 7 The green target spot appears in the antifield position (12 or 6 trials). The monkey is required to make an antifield saccade.

trial type 8 A red spot of light is presented in the antifield direction at 1.5 times the field center eccentricity and extinguishes 120, 170 or 200 msec later. The green spot reappears briefly (20 msec), at a time 20 msec before the red spot disappears, at a distance of 0.25 times the field center eccentricity in the antifield direction (0 or 10 trials). The test is a modification of the experiment designed by Mays and Sparks (1980) to detect quasi-visual neurons. The idea behind it was to entice the monkey into making a saccade to the red flash (even through this was not rewarded) and subsequently to go back to the green flash position (where fixation was rewarded). The distance between red and green flash was made somewhat larger than the field eccentricity because it was observed that the first saccade (to the red flash) was often hypometric. Trials where the first saccade started before both flashes had been presented were discarded.

An example of a neuron which was classified as a quasi-visual cell, based on its neural activity in trial types 1 and 8, is shown in Fig. 3A,B. When the monkey made a saccade to a green target spot in its field, located in the down portion of the right hemifield, we observed a visual response which continued until the saccade began (Fig. 3A). In Fig. 3B it can be seen that the prelude of firing preceding a right-down saccade of about 20 deg was also present when there was no (nor had been any) visual stimulus in the field of the neuron. These responses, the defining characteristic of quasi-visual cells, started shortly (within 50 msec) after the monkey had made a saccade towards the red flash (trial type 8) in the antifield direction (Φ = 105 deg) and continued until the return saccade started.

Eye movements

Eye movements were recorded with the method described by Bour et al., (1984). When adopted for use in monkeys (Van Gisbergen et al., 1985), this method permits a measuring range of about 35 deg in all directions and has an accuracy of 0.25 deg, or better, up to 25 deg eccentricity. The raw eye-movement signals were low-pass filtered (-3 dB at 150 Hz) and digitized with a resolution of 12 bits over a range of 100 deg using a 500 Hz sample rate for each signal. The nonlinearity in the raw eye position signals was corrected off line (Bour

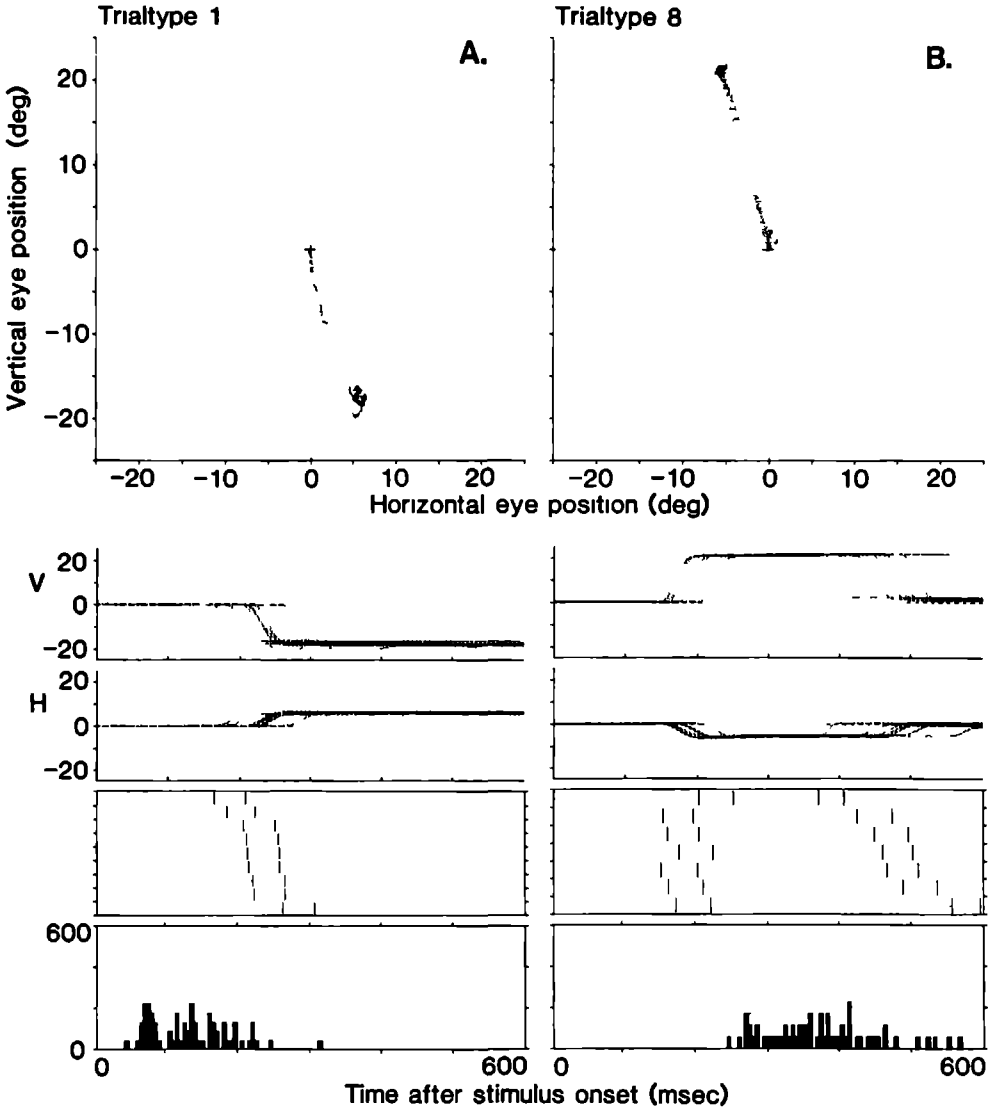

Fig. 3. Responses of a quasi-visual cell A. Responses to green stimulus (trial type 1) in center of receptive field of neuron 11-24-01 located at R = 20 deg and Φ = -75 deg. Other properties of this cell are illustrated in Fig. 7C. The upper half shows the saccade trajectories starting from the fixation point. The lower portion of the figure shows vertical eye position (V), horizontal eye position (H), a dot display of the neural responses, where the vertical marks denote saccade onset and offset, and the mean firing rate histogram. All these plots are made from the same trials. B. Shows behavioural and neural responses of the same neuron in trial type 8. Note that the presentation of the red flash in the antifield position at t=0 did not elicit a sensory response. See text for further explanation.

et al., 1984) based on calibration data from 85 different fixation positions. Saccade detection was performed by a computer program and was subsequently checked by visual inspection of the eye movement record together with the detected onset and offset moments.

Abnormally slow saccades were rejected by requiring that duration (D in msec) remained below some maximum (D_{max}) which depended on saccade amplitude (R, in degrees) according to $D_{max} = 1.3\ R + D_o$. The constant D_o was 32 msec in monkey 10 and 44 msec in monkey 11. Trials in which the first saccade was insufficiently precise were excluded from further analysis. We

required that saccade amplitude should be within 70-140% of the normometric value and that saccade direction and target direction should agree within 20 deg. Slightly more tolerant criteria were sometimes used for neurons with field eccentricities below 5 deg. Finally, trials where latency was less than 80 msec, or where fixation of the central spot was less accurate than 2 deg, were discarded.

Data analysis

To evaluate neuron behaviour in accepted trials, we constructed a dotdisplay in which the spikes were lined up either with respect to stimulus onset or with respect to first saccade onset. The sequence of lines in these displays (see e.g. Figs 4, 5 and 6) does not reflect presentation order in the actual experiment but depends on saccade latency. It was also possible to use saccade duration, saccade amplitude or direction as the criterion for arranging the sequence of trials in the display. The next step was to construct average response histograms from these spike rasters. To highlight the stimulus and saccade-related components in the neural activity separately, responses were summed across trials both relative to stimulus onset and to saccade onset, respectively, and converted into mean time-dependent firing rate (spikes/sec). Binwidth was 5 msec. When the monkey had made both correct and incorrect saccades in a series of double stimulus trials, dotdisplays and mean response histograms were constructed for each stimulus-response combination.

As can be seen in the example of neuron 10-35-01 (Fig. 5C), the firing pattern of the neuron from 50 msec before saccade onset onward was not taken into account in computing the stimulus-locked response histogram. Since saccade latency varied among trials the mean firing rate is based on fewer and fewer trials as time after stimulus onset increases. Similarly, to prevent the initial visual response from distorting the saccade-locked response histogram, the first 100 msec after stimulus onset was left out in computing the mean saccade-related firing pattern. As a result of these variable-epoch averaging procedures, the mean firing pattern for long poststimulus times, or long saccade-lead times, becomes more variable because it is based on fewer trials. The time windows used for stimulus and saccade-related activity were somewhat arbitrary and were a compromise based on what seemed most appropriate for the total population. There are several examples where stimulus-locked discharges seem to continue for more than 100 msec.

Neural data base

Recordings were taken from a total of 123 neurons in the two monkeys. The properties of these neurons as a function of electrode depth and as a function of penetration position within the recording chamber conformed with what is known about the layered and topographical organization of the monkey superior colliculus (Wurtz and Albano, 1980; Robinson, 1972). In one monkey (monkey 10) several penetrations could be confirmed histologically after the experiments. The second monkey (monkey 11) is still in use in a different experiment so that histological data are not yet available.

A total of 43 neurons yielded sufficient data in the double-stimulus experiments to be included in this report.

RESULTS

Behavioural responses

Before we present our neurophysiological data, it is of interest to consider how the monkeys behaved in the target/nontarget experiments. Clearly, the rationale behind the experiments, outlined in the Introduction, would not apply if, in fact, the monkeys would have performed merely at chance level.

Since the overall percentage of correct responses in double-stimulus trials (trials type 2 and 6) was 80% and 97% in the two monkeys, for the data included in this report, performance was very clearly above chance level. It should be added, however, that the behavioural performance of monkey 10 was less than satisfactory in trial type 2 during data collection of 8 neurons, mainly in the first series of experiments. Incorrect responses bringing the gaze to the red stimulus, as in humans (Ottes et al., 1985), occurred mainly when saccade latency was short. When the monkey made such an occasional incorrect response,

this was followed shortly, typically within a few hundred msec, by a second saccade to the target stimulus. As the monkey became well trained, such cross-over responses were very rare in trials where the first saccade was correct. The results from cells obtained when performance was not optimal do not deviate from those collected when the monkey was doing well. Data from these cells will be identified separately when they are used in this paper (see Fig. 10).

Good performance in the target/nontarget task does not necessarily mean that the monkey used the most obvious cue available, namely colour. For example, the system might base its responses on subtle intensity differences between target and nontarget. Although we think this is somewhat far fetched, we did an experiment to check this possibility. In this particular experiment, target and nontarget were both green (Wratten filter 58). The only difference was that the nontarget stimulus had a 0.4 log units higher intensity level. When this experiment was done the monkey (number 11), which did very well in the normal experiment, did not perform above chance level. Another indication that the monkeys were using colour information was the fact that they repeatedly refused to saccade to the suddenly appearing nontarget stimulus in trials type 4 and 8 (see Methods). This was most often seen in monkey 11, especially when the previous trials also contained a nontarget stimulus. Thus, although nothing can be said on a trial by trial basis, we conclude that for the majority of the experiments described in this paper, the monkeys probably used colour information.

Neurophysiological data

In order to facilitate discussion of our data, we have classified our cells into 3 major groups, based on the following criteria:

1. Visual cells. This class comprises all cells where the neural activity reflected the presence of a sensory receptive field, did not show a saccade related burst, and were not recruited in trial type 8.
2. Quasi-visual cells. These cells have a visual receptive field, have sustained activity before the corrective saccade which returns the gaze near the primary position in trial type 8 (see Figs 2 and 3) but lack a clear saccade-related burst. Because in early experiments trial type 8 was not included, the number of quasi-visual cells may have been underestimated. Furthermore, animal performance was not always as we had intended in this task. For example, the monkey sometimes refrained from making a saccade to the red nontarget stimulus. This is a further reason why some cells classified as visual may in fact have been quasi visual.
3. Visuomotor cells. These cells responded to visual stimuli in their field and had a burst of activity before and during a saccade toward a stimulus in their visuomotor field. Pure motor cells (lacking visual responses) were not observed in our sample (see Fig. 10).

Based upon these criteria, the distribution in these categories was as shown in Table 1.

Table 1. Classification of SC cells

class	number of cells
visual	24
quasi visual	3
visuomotor	16
total	43

Saccade-related activity

One objective in our experiments was to determine whether SC movement cells participate in the generation of saccades in double-stimulus trials requiring target identification based on colour in the same way as they are involved in the generation of saccades to a single visual stimulus. If they are, a saccade-related burst should be observed for all saccades to a visual stimulus in the visuomotor field. If the single target relation would not hold for double-stimulus trials, the possibility that the relevant signals reach the brainstem saccade generator by an extracollicular pathway should be seriously considered (see Introduction). With this in mind it is now appropriate to have a close look at the result ob-

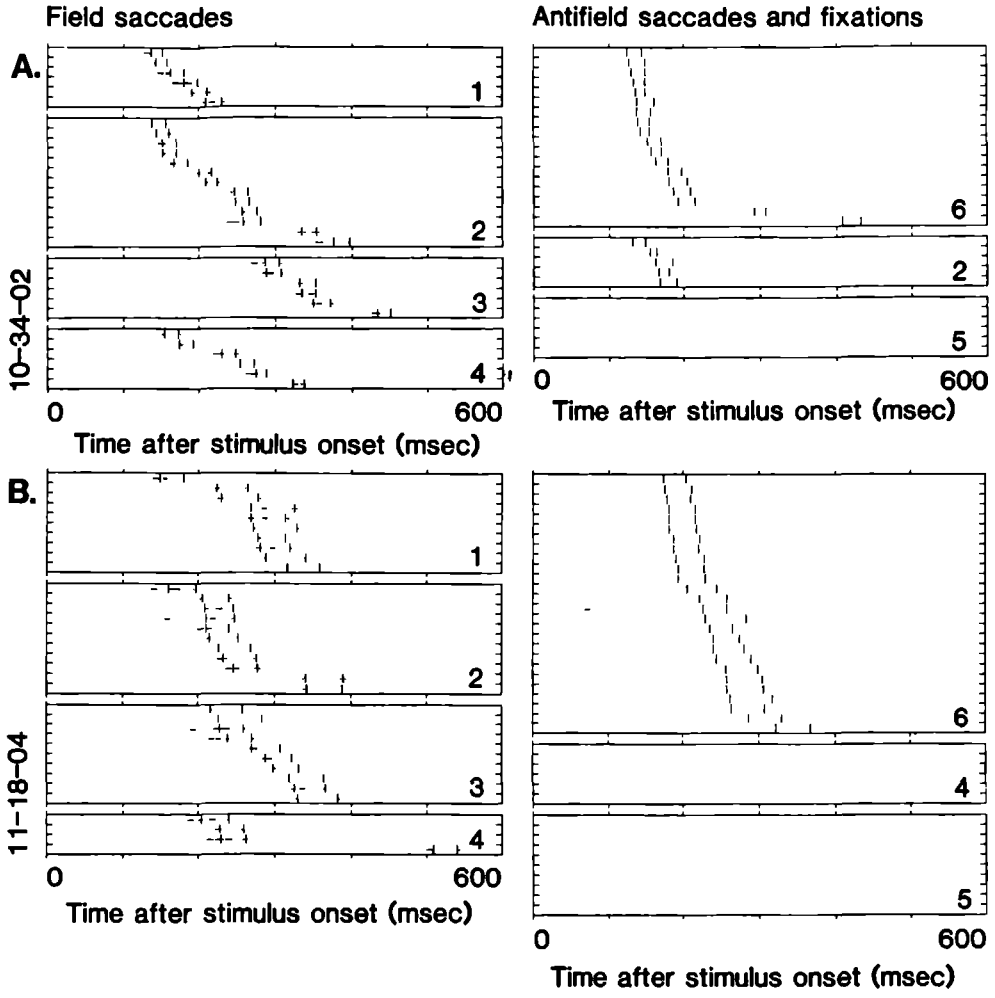

Fig. 4. Responses of visuomotor cells A. Responses of neuron 10-34-02 in trials which led to field saccades (left-hand side), to antifield saccades (right-hand side; 2 upper panels) or no saccade at all (right-hand side; lower panel). Number in each panel identifies trial type (see Methods and Fig. 2). The center of the visuomotor field of this neuron was located at R = 3 deg and Φ = 30 deg. B. Responses of neuron 11-18-04; same conventions as in A. The center of the visuomotor field was located at R = 15 deg and Φ = -15 deg. Unlike in A, in this cell's data-set there are no incorrect saccades in double spot trials. Therefore, in this cell, panel 2 is only on the left. Note that panel 4 appears on both sides. The left-hand panel 4 contains those catch trials which led to a field saccade. In right-hand panel 4, the monkey maintained gaze position after the green fixation spot (scene 1; Fig. 2) extinguished and ignored the red stimulus at least in the 600 msec period shown. Note that the activity seems different in panels 4 and 5, although gaze was maintained in both (right-hand side; see Results).

tained from two typical SC movement cells (Fig. 4A,B).

In Fig. 4A,B, the various panels contain responses to trials which resulted in a saccade towards a visual stimulus in the visuomotor field (field saccade; left hand side) or in a saccade in the opposite direction (antifield saccade; right hand side) or in a fixation (right-hand panel, below). The number in each panel refers to the type of trial (see Methods). In Fig. 4A, the upper panel (1) shows the activity of the neuron when the monkey made a saccade toward the single green spot presented in the center of the visuomotor field. There is

an initial weak stimulus locked response, with a latency of some 50-60 msec, followed by a saccade-related discharge. The vertical marks in each line denote first saccade onset and offset. Similar saccade-related bursts can be seen in the other panels '2,3,4' although the stimulus conditions were quite different. In trial type 2, for example, the target was presented in the visuomotor field together with the nontarget stimulus at the antifield position. If, and only if, the monkey made a saccade to the field stimulus was a saccade-related burst observed. This can be appreciated by comparing panel 2 on the left hand side 'correct saccades) and on the right hand side 'incorrect saccades to nontarget stimulus). That the burst is really related to saccade direction, irrespective of whether this led to foveation of a red or a green stimulus, can be deduced from panel 4 'saccade to red catch stimulus in field) and panel 6 'correct saccades to green spot in antifield). In panel 3 'red spot in primary position; green in field) saccades had quite long latencies but all had a burst associated with them. Finally, when the monkey did not make a saccade at all, although the red stimulus was present in the field (panel 5; fixation trial) no burst activity was observed. A quite similar picture emerges in Fig. 4B. Also in this visuomotor cell all field saccades are accompanied with a saccade-related burst. By contrast, the antifield saccades, made in the target/nontarget trials portrayed in panel 6, do not show a single example of a clear movement-related burst. Thus, at least qualitatively, these examples show activity patterns compatible with what might be expected if the colour information affects the saccadic system at or above the level of SC visuomotor cells, at the time the saccade is generated.

To evaluate the behaviour of these neurons more quantitatively, we have computed average perisaccade histograms for each condition using the variable-epoch averaging technique outlined in the Methods section. A typical result is illustrated in Fig. 5C. The dot displays of the various stimulus-response combinations for this cell (Fig. 5A,B) show the same overall pattern as the cells in the previous figure 'Fig. 4A, B). We point out, however, that there is one trial 'panel 2; Fig. 5A) where a correct field saccade to the green stimulus occurred without a clear burst. This was not due because the saccade was not goal directed (it was) but might be a rather rare example of a trial where the serial hypothesis 'see Introduction) was violated. Very occasionally, similar examples have been observed in other cells. Remarkably, the opposite possibility for violation of this hypothesis - a burst together with an antifield saccade - was never seen. The fact that the saccade without a burst referred to above was slower than normal may be relevant. We have seen other examples where the burst became less vigorous and later relative to saccade onset when saccade duration was somewhat prolonged.

In Fig. 5D the mean perisaccade histogram computed from the data in panel 2 (Fig. 5A,C) is shown together with similar histograms from panels 1, 3 and 4. As can be seen, the saccadic burst profile is quite similar in all cases, despite the rather profound differences among the various tasks in which these data were obtained. The histograms for the antifield saccade data in Fig. 5B are not shown, since under these conditions the cell was simply completely silent when the saccade was made.

In the previous section we compared SC movement cell activity associated with saccades made in intermingled single and double-stimulus trials. Although this is a fair comparison to make, it is possible that the single target results would be different if they had been collected in a separate experiment. After all, if there is a rather high probability that the next trial will require a two-stimulus discrimination, the mental settings of the animal may well be different, and these might have an effect. Therefore, we measured neural activity of a few SC movement cells while the monkey made a series of saccades to a repetitive stimulus in the visuomotor field. This was done in order to make the task of executing a visually guided saccade as "automatic" as possible. To discourage the generation of anticipatory saccades, timing of the identical target displacements was randomized. The results are shown in Fig. 6A,B,C,D.

The neural activity patterns measured in the easy repetitive task and in the difficult task are qualitatively very similar. It appears, however, that the motor-related activity

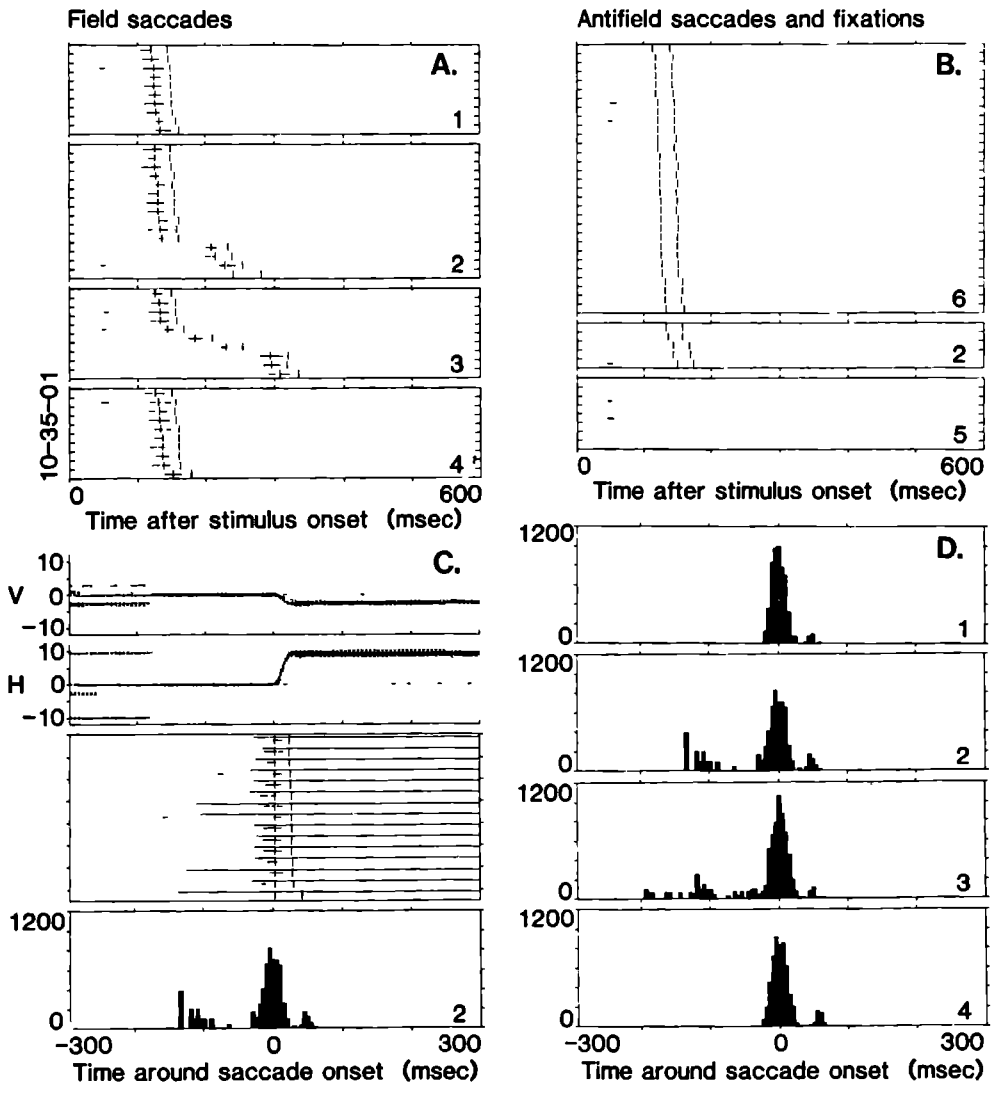

Fig. 5. Independence of field-saccade burst upon trial type in a typical visuomotor neuron. A. Activity of cell 10-35-01 for field saccades elicited by trial type 1,2,3 and 4. The saccade-related discharge looks similar in all four conditions. Field location: R = 10 deg; Φ = -15 deg. B. Activity of the same cell associated with antifield saccades in trials type 2 and 6 (2 upper panels). Panel 5 shows neural activity during fixation responses in trials of type 5. C. Illustration of how mean perisaccade histogram was computed from panel 2 responses in A. Spike rasters have been aligned horizontally with saccade onset and ordered vertically depending on saccade duration. Line above each series of dots indicates epoch which was used for computing the mean rate shown below (see Methods). Since the number of epochs used in computing this mean decreases with time before the saccade, this goes along with a concomittant increase in variability. The upper part shows the horizontal (H) and vertical (V) eye position signals. Note that one saccade was slower (see text). D. Mean time-dependent saccade burst rates computed from panels 1,2,3 and 4 (in part A) using the method illustrated in C. Panel 2 shows the same histogram as in C. Note that the saccadic burst seems independent upon the stimulus conditions.

of the neuron is somewhat higher in the repetitive task (Fig. 6C,D). We found no indication for qualitative differences among the various types of trials (1, 2 and 3) in the difficult task. Therefore, these were pooled in Fig. 6D.

Similar results were found in a few other visuomotor neurons which were tested in the same way. While these results do not prove anything, they indicate at least that quantitative differences in neuron behaviour may be caused

by a change in system settings to optimize performance when task requirements change. They also indicate that these effects are relatively minor.

Saccade prelude activity

We will now present our findings on the activity of SC neurons in the interval between about 100 msec after stimulus onset and 50 msec before the saccade. This period will be denoted as saccade prelude interval (prelude, for short). Even though saccades do not occur in fixation trials (trial type 5) the term prelude in this case will be used to refer to the time span which in other types of trials preceeds a saccade.

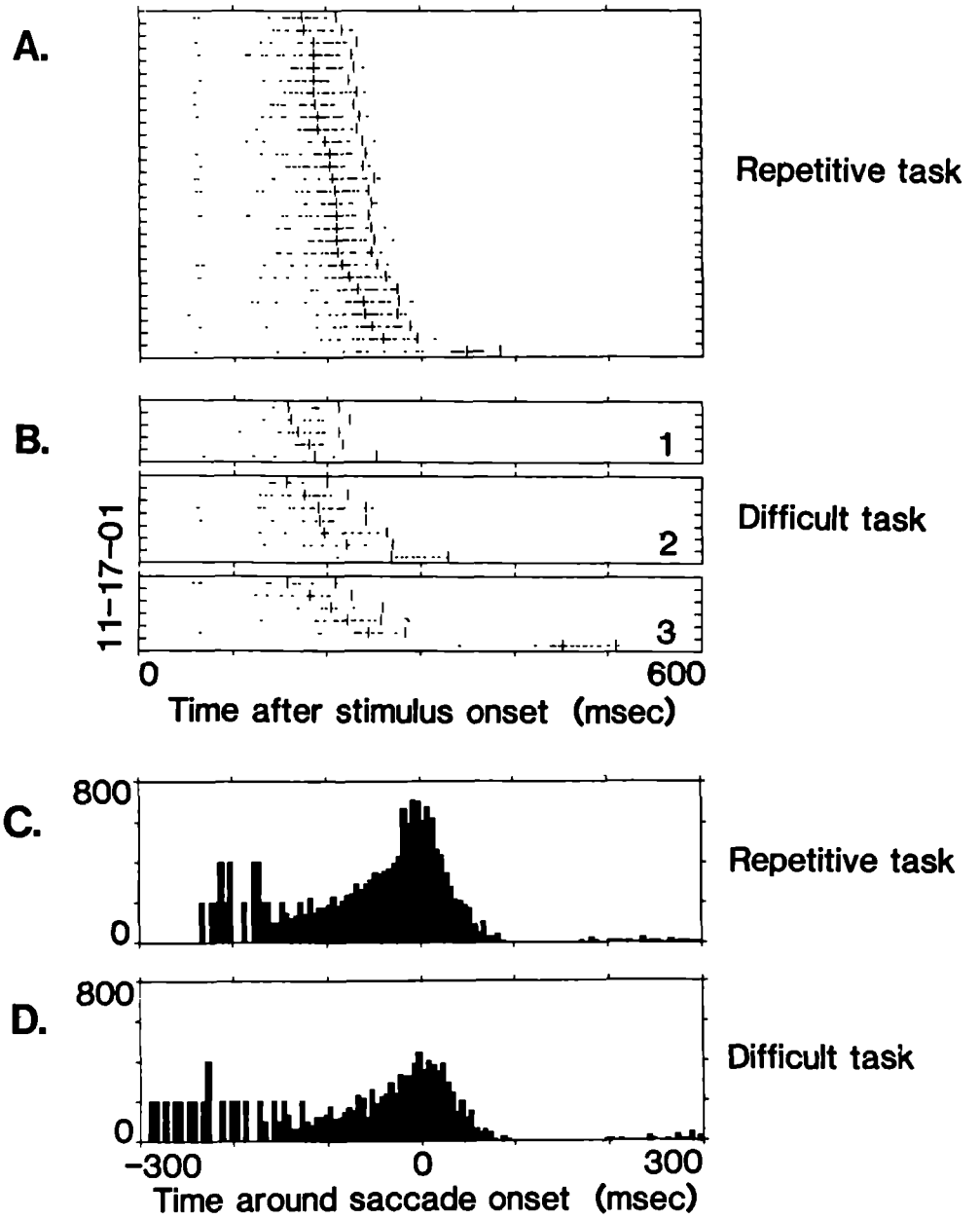

Fig. 6. Effect of predictibility in task. A. Responses of visuomotor neuron 11-17-01 associated with field saccades elicited by a repetitive (predictable) field stimulus. Field location R = 25 deg; Φ = -20 deg. B. Responses of the same neuron associated with field saccades made in trials type 1,2, and 3. C. Mean perisaccade histogram computed from responses in A. D. Mean perisaccade histogram computed from pooled responses in B.

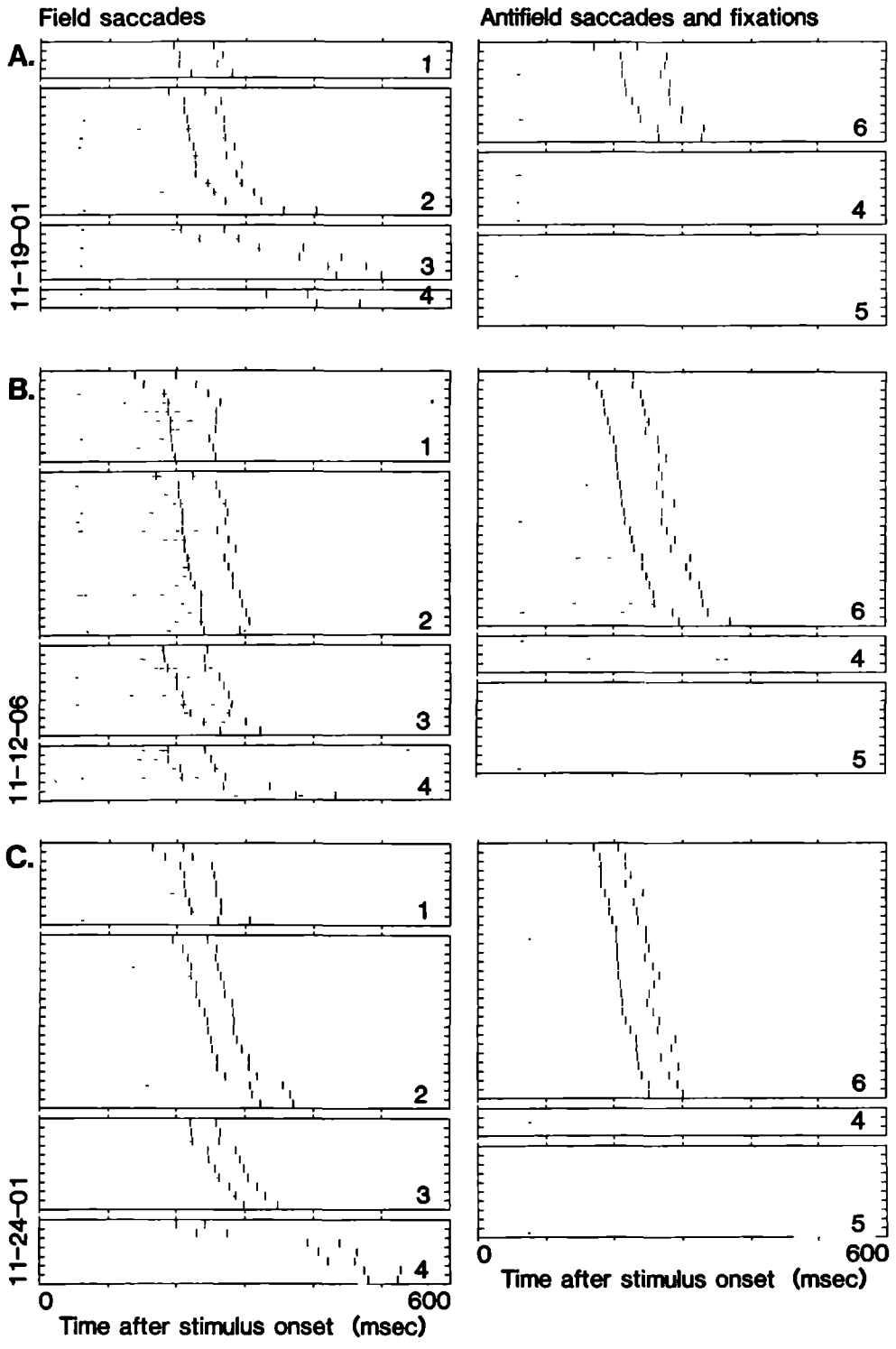

Fig. 7. Trial dependence of saccade prelude firing rate (definition: see text). Panels on the left-hand side show activity preceding field saccades (panels 1,2,3 and 4). On the right-hand side, antifield saccade-related activity is shown (panel 6) together with continuing fixation responses in trial types 4 and 5 (panel 4 and 5). A. Neuron 11-19-01, classified as quasi-visual. Field location at R = 25 deg and Φ = -45 deg. This neuron is our clearest example for showing enhancement as defined by Wurtz and Mohler (1976). The cell seems to meet requirement 1 (see text) since the prelude activity in panels 1,2 and 4 is (nearly) equal. Since the prelude rate in panel 6 is clearly less, requirement 2 (see text) is also met. Furthermore, it

Prelude firing rate is of interest for the purpose of our study because the neural activity occurring between the presentation of the stimulus and the motor response may be related to target selection. Wurtz and Mohler (1976) found that under certain experimental conditions, some SC neurons showed a stronger response to a visual field stimulus when it was used as a target for a saccade than when it was not. They called this phenomenon late enhancement. In exploring the possibility that similar phenomena, might also be present under our conditions, we required that the cell's prelude rate in the various types of trials must fulfil a number of requirements. We will use the prelude rate of the neuron when the monkey makes a field saccade to a green target stimulus in the field (trial types 1,2 and 3) as the yard stick with which the activity in other conditions will be compared. We will denote this as the green prelude rate. The requirements, which we felt should be met before it can be concluded that variations in prelude rate with trial and response type may be linked to target selection were as follows:

First, when the red nontarget stimulus in catch trials attracts a saccade the prelude rate should equal the green prelude rate. In other words, the colour of the stimulus which attracts a field saccade should be irrelevant. If the spectral properties of the field stimulus affect the firing rate in the prelude preceding the targeting saccade, this may simply be the consequence of somewhat different visual responsiveness to red and green.

Second, when in trial type 6 a red field stimulus is not used as a target for a saccade because the monkey foveates the green stimulus in the antifield position, the prelude rate should be less than the green prelude rate.

Third, the prelude rate should also be less than the green prelude rate if a red field stimulus is being ignored by the saccadic system when the monkey maintains central fixation (trial type 5).

Fourth, the prelude rate when the monkey saccades to a green target spot in the field while a red nontarget spot is presented at the primary position should equal the green prelude rate. If this requirement is met, it is improbable that the reduction in prelude rate required in trial type 5 (requirement 3) is somehow due to the presentation of a foveal stimulus rather than to withholding a saccadic response to the field stimulus.

We have analyzed prelude firing rates by inspecting dot displays like in Figs 4A,B and 5A, B. In 30 cells sufficient responses were available in each essential category and with a sufficiently wide range of saccade latencies to judge the neuron by each of the four criteria. In the other cells this was not possible because the monkey had not made a sufficient number of catch saccades, or because the prelude interval was too short due to short response latencies.

The overall impression gained by applying our criteria upon this material is that there is some evidence for enhancement in a small group of cells. We found that at most seven cells in the group of 30 neurons investigated (23%) met all four criteria. Thus, these neurons (four visuomotor, two quasi-visual, one visual cell) are potentially involved in target selection. We emphasize that these cells got into this category only by a narrow margin so

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is obvious that the prelude rate in panel 5 (fixation) remains below that in panels 1 and 2, so that requirement 3 (see text) is met. Finally, the prelude rate in panel 3, left hand side, is very similar to the prelude rate in panels 1,2 (requirement 4). Note that even our best enhancement unit still leaves room for doubt (requirement 1). B. Neuron 11-12-06, classified as visuomotor. Field location at R = 30 deg and Φ = -75 deg. This cell meets requirement 1 (prelude rate panels 1,2 = prelude rate panel 4, left-hand side); requirement 3 (prelude rate in fixation trial type 5 is less); requirement 4, see text (prelude rate in panel 3 equals that in panels 1,2). Requirement 2 is also met (prelude rate in panel 6 is less than in panels 1,2) but the difference is very small. Note however that this difference suddenly becomes very clear just prior to saccade onset. C. In this neuron (cell 11-24-01; quasi-visual; field location at R = 20 deg, Φ = -75 deg) requirement 1 is not met; the other requirements are. The type of evidence used to classify this cell as quasi visual is shown in Fig. 3.

that the number found definitely constitutes an upper bound. How this margin could be narrow for one criterion, but quite wide for the others can be appreciated by inspecting Fig. 7A, which represents one of the cells with the best evidence for enhancement. The prelude rate of this cell when a red field stimulus was ignored, such as in panel 5 (fixation) and in panel 6 (saccade to green target in antifield), was clearly less than when a green (panels 1,2, 3) or a red field stimulus (panel 4) was used as a saccade target. The data of this cell meet requirements 2, 3 and 4 without any problem. Deciding criterion 1 was more delicate because *the catch-saccade prelude rate (panel 4)*, although clearly enhanced relative to conditions where red did not attract a saccade, may actually still be slightly less than when the saccade is attracted by a green field stimulus (panels 1,2).

Another cell which marginally fits the four criteria (Fig. 7B) had very sustained activity before the returning saccade in the test designed to detect quasi-visual cells (trial 8). Somewhat arbitrarily, the cell was classified as visuomotor, not as quasi visual, since it appears to have (weak) motor related activity. As can be noticed, this cell has clearly less prelude activity when a red field stimulus is used for a targeting saccade (panel 4; catch saccades) than when it is not, when the monkey is fixating a green spot (panel 5). The reduction in prelude activity when the red stimulus is being ignored in trial type 6, where the monkey saccades to the antifield green stimulus is, however, extremely small (panel 6). The figures discussed so far (Figs. 7A,B), are intended to convey that interesting effects in the prelude activity can be observed in some cells, but also that these correlates with impending motor events are not nearly as convincing as those contained in the motor-related activity proper.

Among the other cells, which did not meet all four requirements, we sometimes saw prelude activity *which seemed both determined* by stimulus colour and the behavioural response (seven cells). Since our four criteria require, in essence, that the behavioural response should be the only determining factor, these cells do not have enhancement in the strict sense. To illustrate what we mean, examples are shown in Figs.

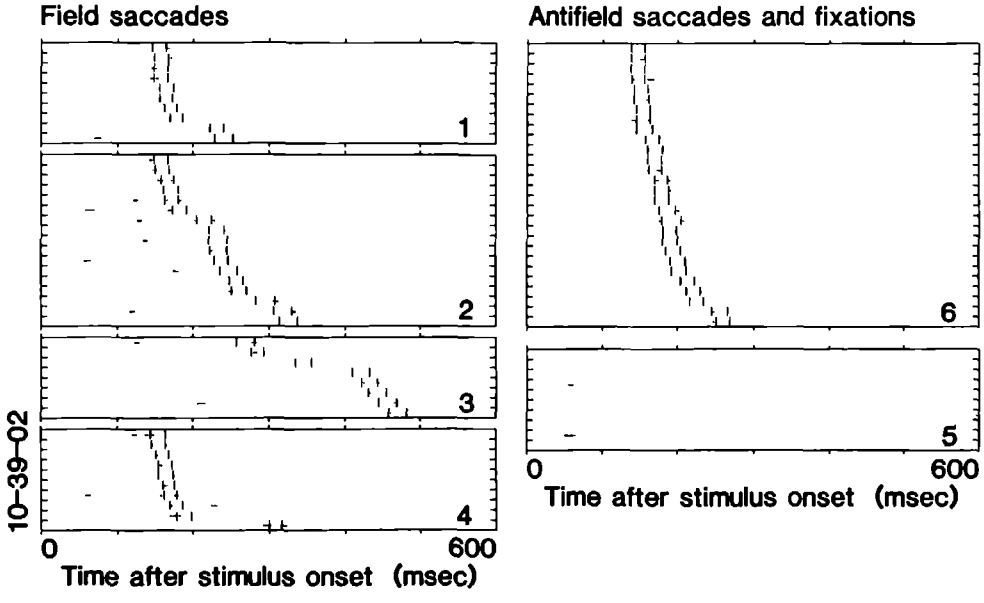


Fig. 8. Responses of a visual neuron. Activity of the neuron (cell 10-39-02) associated with field saccades is shown in four panels on the left-hand side. Activity associated with antifield saccades (panel 6) and fixation (panel 5) is shown on the righthand side. Field location at R = 4 deg and Φ = 10 deg. This cell has the same prelude activity for field saccades and antifield saccades and thus fails to meet requirement 2 for showing enhancement. The neuron meets the other requirements.

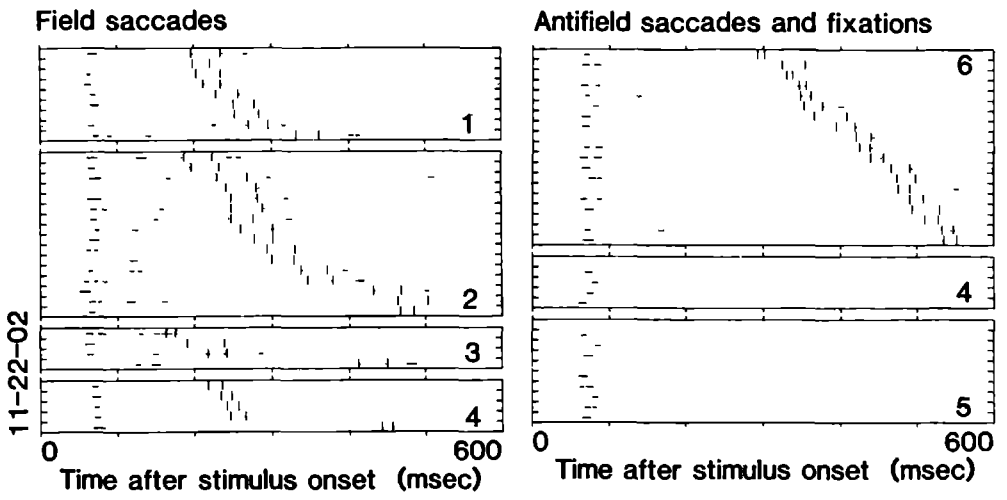


Fig. 9. Responses of a visual neuron. Same conventions as in Fig. 8. Cell 11-22-02. Field location at R = 3 deg, Φ = 75 deg.

7C and 8. Inboth cells, as in all other cells in this subclass, requirement 3 (fixation prelude rate should be less than the green prelude rate) is met. The cell in Fig. 8 does not meet any other requirement. By contrast, the cell in Fig. 7C (a quasi-visual cell) meets also requirements 2 and 4. However, since the prelude rate preceding catch saccades (panel 4) is lower than the green prelude rate (panels 1,2), requirement 1 is clearly not met.

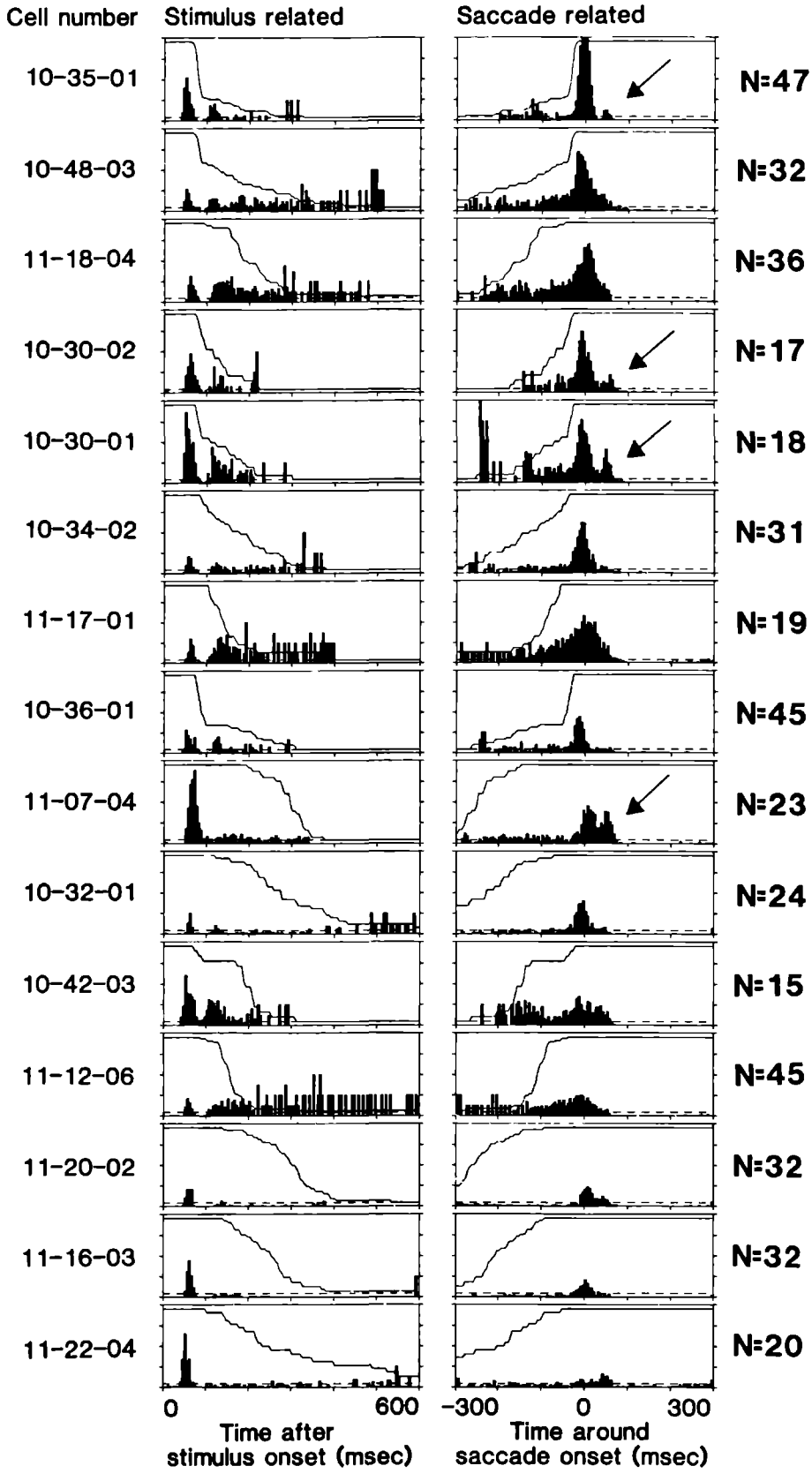
It has been hypothesized by Mays and Sparks (1980) that quasi-visual cells code motor error. If they do also under our experimental conditions, one would expect that their prelude rates should conform with each of the four requirements we have made. Of the three quasi-visual cells in our sample, two cells met all and one cell met three requirements. This is clearly an interesting area for further research.

Finally, a total of 16 cells (53%) did not show any sign betraying a potential role in target selection. Of these, one group of six cells met criterion 1, failed to meet criteria 2 and 3 and met criterion 4 (code: +, -, -, +). These were purely visual cells with equal responsiveness and an equal time course of response to a red or a green field stimulus, completely independent on whether or not a saccade was made and, if it was made, independent on its metric properties. The other group of nonremarkable cells, where application of the criteria yielded (-, +, + or -), consisted of 10 purely visual cells which had a somewhat lower sensitivity for red than for green field stimuli (Fig. 9). Their prelude activity for catch saccades to a red stimulus in the field was the same as when the monkey ignored the red field stimulus (trials type 5 and 6). The only reason, then, why these cells met requirements 2 and 3 was their slightly lesser red sensitivity. We stress that, although the magnitude of the response to red and green might differ somewhat, the responses were qualitatively the same. Therefore, all cells fell in the category of colour-nonopponent neurons.

Stimulus-related activity

The cells in our sample typically responded to the red or the green stimulus in their field with a latency of some 50-60 msec. After the initial burst most cells (about 75%) paused and thereafter showed a lower spike rate than in the initial burst. Examples of neurons with and without the pause are shown in Figs. 8 and 9, respectively.

The initial visual burst, followed by a more or less clear pause, was also present in cells with a saccade-related discharge. Its relative strength varied appreciably from cell to cell (Fig. 10). In a few cells we observed a post-saccadic burst which may have been an off response due to the saccade which wiped the visual stimulus off the field (see also Fig.9).


Cell number
Stimulus related
Saccade related
10-35-01
N=47
10-48-03
N=32
11-18-04
N=36
10-30-02
N=17
10-30-01
N=18
10-34-02
N=31
11-17-01
N=19
10-36-01
N=45
11-07-04
N=23
10-32-01
N=24
10-42-03
N=15
11-12-06
N=45
11-20-02
N=32
11-16-03
N=32
11-22-04
N=20
0
600
Time after stimulus onset (msec)
-300
0
300
Time around saccade onset (msec)

It is known from work in anesthetized paralyzed monkeys that cells with both an on and an off response to visual stimuli are quite common in the SC (see e.g. Moors and Vendrik, 1979). Examples of these late bursts in visuomotor neurons have been, marked by arrows in Fig. 10. In these cells the early stimulus-related discharge was quite strong.

In none of the cells which were investigated with red and green stimuli could a clear indication of colour-opponent properties be found. That is, the response to the red and green stimulus was always qualitatively the same (see Fig. 4 through 9).

Out of 38 cells, where good quantitative comparison could be made, 33 (87%) had the same strength and timing of response to red and green stimuli in the first 100 msec after the stimulus. The rest of these cells (5/38) had a somewhat weaker red onset response. The response to red in the cells which had initially no red/green difference was sometimes observed to be more transient later on. An example can be seen in Fig. 9. This red/green difference was related entirely to which stimulus was in the receptive field, independent of the behavioural response (e.g. catch versus fixation trial). Accordingly, this difference must reflect the visual properties of the neuron (see section on saccade prelude activity) and appears unrelated to participation in the target selection process.

DISCUSSION

1. General comments

The results of our experiments show that, in a task based on colour discrimination, SC movement cells have roughly the same saccade-related activity as in more classical simple tasks. Since SC visual neurons seem to lack virtually all capacity to analyze fine grain spatial detail (Cynader and Berman, 1972), a study with a quite similar logic could probably be done by relying on a shape cue to make the target/nontarget distinction. In this way the difficulty of having to perform a colour brightness match can be avoided.

What does it mean that SC movement neurons maintain about the same relation between burst activity and saccade metrics when the monkey shifted from a simple to a complex task? Our results clearly suggest the possibility that the SC participates in the generation of visually guided saccades also when this requires more sophisticated signal processing then merely detecting a single visual stimulus on a homogeneous background. Apparently, SC movement cells somehow have access to signals from the perceptual visual system. To determine how essential the SC role is will require lesioning or reversible inactivation experiments.

We now wish to point out two seemingly paradox elements in the results. First, the population activity of SC movement cells has a strong correlation with the responses made by the total system in the target/nontarget task, but only in the interval just prior and during the saccade. At that time therefore the visuomotor cell, just as the total system, can discriminate colour. Second, by contrast, before this period it would be difficult to predict, by monitoring the activity of the entire population of SC cells, how the saccadic system will respond in any particular trial. The initial response to green and red field stimuli was qualitatively and quantitatively identical

Fig. 10. Stimulus-related and saccade-related activity in visuomotor neurons. Stimulus-related activity is shown in the left-hand column. The right-hand column represents saccade-locked activity of the same neurons. The vertical scaling in all histograms reaches from 0-800 spikes/sec. Binwidth is 5 msec. The thin line in each histogram indicates the relative running number of contributing trials. The histograms shown were obtained from trials yielding fieldsaccades. Data were pooled across trials 1,2,3,4, 5 and 6. There appears to be no clear relation between the strength of the motor burst and the strength of the initial visual response. As can be seen, in most visuomotor neurons the initial visual response consists of a short burst followed by a pause. Arrows indicate post-saccadic burst discussed in text. The figure contains a few cells where monkey performance during data collection was not entirely satisfactory (see Results section on behavioural data). These cells were: 10-30-01, 10-30-02 and 10-48-03.

in the majority of cells, SC visuomotor cells included, and would be an entirely useless predictor of impending sacccade behaviour. The prelude activity, defined above, likewise could be a poor predictor in the large majority of cells. Thus, interestingly, our data confirm earlier work (Marocco and Li, 1977) claiming that the collicular visual system lacks the ability to analyze colour, yet shows convincingly the SC involvement in a colour discrimination task. If SC visuomotor cells behave as if they are colour blind until their saccadic burst begins, how do they obtain the crucial colour information? This problem will now be discussed in detail.

2. Access of cortical colour information to motor colliculus

We regard our results as a corroboration of hypothesis 2 outlined in the Introduction. This hypothesis implies that cortical colour information, originating ultimately from area 17, must somehow be able to influence SC movement cells. We will discuss various anatomical pathways which might embody connection 2 in the black-box diagram of Fig. 1.

A) A first possibility to be considered is the striate visual cortex (area 17)-SC pathway. The area 17 cells projecting to the SC are in layer 5. (Finlay et al., 1976). It has been shown that reversible inactivation of area 17 by local cooling does not affect the properties of SC superficial layer cells but yields deeper layer cells unresponsive to visual stimulation (Schiller et al., 1974). Although these corticotectal cells may be important in any visually guided saccade task, they are unlikely to carry the colour information in our double stimulus paradigm. It has been demonstrated by reversible inactivation of separate layers in the lateral geniculate nucleus (Schiller et al., 1979) that the corticotectal cells are driven exclusively from the magnocellular layers which are known to contain colour-nonopponent cells.

B) In extrastriate visual cortex, Fischer and coworkers (Fischer and Boch, 1981; Fischer et al., 1981) have found presaccadic enhancement. The region investigated probably corresponded with visual area V4, a region which seems to have at least some capacity for extracting colour information (for a review, see Desimone et al., 1985). Although there is no evidence that the enhancement observed is specific for saccades, signals from this region might conceivably be of importance for SC neurons by way of corticotectal connections (Fries, 1985).

C) A further cortical area of potential interest concerns area 7 in the posterior parietal cortex. Visually responsive cells in this area show enhanced responsiveness when the animal pays attention to the stimulus such as when it is used as a target for a saccade (Lynch et al., 1977; Bushnell et al., 1981). Bushnell and coworkers have shown that parietal cortex enhancement, unlike collicular and frontal eye field enhancement, is not specifically related to saccades. Electrical stimulation in the posterior parietal cortex of the monkey causes saccadic eye movements (Shibutani et al., 1984). Since parietotectal projections connect this region with the intermediate and deep layers of the colliculus (Lynch et al., 1985), SC visuomotor neurons may have access to these signals. It is not known, however, whether the parietal cortex neurons can really make the colour distinction needed in our experiments.

D) Naturally, we also have to consider the possibility that the frontal eye fields (area 8) somehow mediate the colour information. In this region, cells show enhancement specifically related to saccades (Goldberg and Bushnell, 1981). It has been remarked (Bruce and Goldberg, 1985), however, that these neurons do not respond differentially to colour stimuli. So far, the activity of frontal eye field neurons has not been studied in a saccadic colour discrimination task. Our experience with collicular neurons shows that the fact that visual responses are spectrally nonopponent does not preclude that movement-related activity may be based on colour information. To explore the possibility that the frontal eye fields furnish the colour information to SC visuomotor cells, it would be necessary to investigate the effect of frontal eye field inactivation on the execution of our task. There are

several possibilities how the frontal eye fields could affect the SC activity which we have measured. Leichnetz et al. (1981) have demonstrated a direct connection to the intermediate layers of the SC. An alternative pathway through the substantia nigra, pars reticulata, will now be discussed in more detail.

3. Possible role of the substantia nigra in target selection

The preceding Discussion section has been added to emphasize that there are several corticofugal pathways, not necessarily involving the frontal eye fields, which may give the saccadic system access to the stimulus information it needs in our task. Recently, it has been suggested that the substantia nigra SN), pars reticulata, probably plays a role in the generation of saccade-locked activity of collicular movement-related cells (Hikosaka and Wurtz, 1983a,b, 1985a,b). The SN is part of at least one of the several corticofugal oculomotor pathways discussed above. The studies by Hikosaka and Wurtz seem of interest, then, in particular because they suggest a mechanism by which signals of cortical origin can influence collicular signal processing. Hikosaka and Wurtz (1983a) have presented evidence that both visual as well as saccade-related SN neurons project to SC intermediate layers. Some of these SN neurons, which normally have a high steady firing rate, paused briefly when SC neurons with similar field locations showed a saccade-related burst. It was hypothesized that these SN pause cells help to create the saccadic burst in SC neurons by disinhibition. If we wish to apply this idea to our situation, we have to assume that the SN saccadic pause cells gated the SC visuomotor cells also under our experimental conditions. Of course, to create a burst of activity, merely releasing the SC neuron from tonic SN inhibition is not sufficient: a source of excitation is also needed. This could be an intrinsic tonic excitation from collicular origin. Another possibility has been discussed by Hikosaka and Wurtz (1983a).

The idea that an external gating signal - a sudden, brief release from tonic SN inhibition - creates the SC visuomotor neuron burst in our target/nontarget paradigm is speculative but attractive. It would explain nicely why the correlation between neural activity and saccade metrics can be very good just prior and during saccades, but not longer before the saccade. The prelude activity in SC visuomotor neurons would then be the result of the hypothetical tonic drive still kept in check, both on the target and the nontarget location in the collicular map, by continuous SN inhibition.

The second type of SN cells projecting to the SC, visual cells showing enhancement, are of potential interest to explain the (weak) enhancement effects in some of our neurons. These SN neurons have enhancement in the sense that the pause caused by a visual stimulus in their receptive field was more pronounced when the stimulus was used as a target for a saccade than when it was not, such as when the monkey made a saccade to a stimulus outside the field, or maintained fixation (Hikosaka and Wurtz, 1983b). Since the pause had rather long onset latency (mean 120 msec; Hikosaka and Wurtz, 1983b), these cells could influence SC neurons in the saccade prelude (see above) but not during the initial stimulus related response. To explore these ideas further, recordings from substantia nigra neurons will have to be made in animals engaged in our stimulus paradigm.

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REFERENCES

Albano JE, Mishkin M, Westbrook LE, Wurtz RH (1982) Visuomotor deficits following ablation of monkey superior colliculus. J Neurophysiol 48: 338-351

Bour LJ, Van Gisbergen JAM, Bruijns J, Ottes FP (1984) The double magnetic induction method for measuring eye movement - results in monkey and man. IEEE Trans Bio-Med Eng BME 31: 419-427

Bruce CJ, Goldberg ME (1985) Primate frontal eye fields. I. Single neurons discharging before saccades. J Neurophysiol 53: 603-635

Bruce CJ, Goldberg ME, Bushnell MC, Stanton GB (1985) Primate frontal eye fields: II. Physiological and anatomical correlates of electrically evoked eye movements. J Neurophysiol (in press)

Bushnell MC, Goldberg ME, Robinson DL (1981)

Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention. J Neurophysiol 46: 755-772

Cynader M, Berman N (1972) Receptive-field organization of monkey superior colliculus. J Neurophysiol 35: 187-201

Desimone R, Schein SJ, Moran J, Ungerleider LG (1985) Contour, color and shape analysis beyond the striate cortex. Vision Res 25: 441-452

Finlay BL, Schiller PH, Volman SF (1976) Quantitative studies of single-cell properties in monkey striate cortex. IV. Corticotectal cells. J Neurophysiol 39: 1352-1361

Fischer B, Boch R (1981) Enhanced activation of neurons in prelunate cortex before visually guided saccades of trained rhesus monkeys. Exp Brain Res 44: 129-137

Fischer B, Boch R (1983) Saccadic eye movements after extremely short reaction times in the monkey. Brain Res 260: 21-26

Fischer B, Boch R, Bach M (1981) Stimulus versus eye movements: comparison of neural activity in the striate and prelunate visual cortex (A17 and A19) of trained rhesus monkey. Exp Brain Res 43: 69-77

Friendlich AR (1973) Primate head restrainer using a nonsurgical technique. J Appl Physiol 35: 934-935

Fries W (1984) Cortical projections of the superior colliculus in the macaque monkey: a retrograde study using horseradish peroxidase. J Comp Neurol 230: 55-76

Fuchs AF, Kaneko CRS, Scudder CA (1985) Brainstem control of saccadic eye movements. Ann Rev Neurosci 8: 307-337

Goldberg ME, Bushnell MC (1981) Behavioral enhancement of visual responses in monkey cerebral cortex. II. Modulation in frontal eye fields specifically related to saccades. J Neurophysiol 46: 773-787

Guitton D, Buchtel HA, Douglas RM (1985) Frontal lobe lesions in man cause difficulties in suppressing reflexive glances and in generating goal-directed saccades. Exp Brain Res 58: 455-472

Harting JK (1977) Descending pathways from the superior colliculus: An autoradiographic analysis in the rhesus monkey (macaca mulatta). J Comp Neurol 173: 583-612

Hikosaka O, Wurtz RH (1983a) Visual and oculomotor functions of monkey substantia nigra pars reticulata. I. Relation of visual and auditory responses to saccades. J Neurophysiol 49: 1230-1253

Hikosaka O, Wurtz RH (1983b) Visual and oculomotor functions of monkey substantia nigra pars reticulata. IV. Relation of substantia nigra to superior colliculus. J Neurophysiol 49: 1285-1301

Hikosaka O, Wurtz RH (1985a) Modification of saccadic eye movements by GABA-related substances. I. Effect of muscimol and bicuculline in monkey superior colliculus. J Neurophysiol 53: 266-291

Hikosaka O, Wurtz RH (1985b) Modification of saccadic eye movements by GABA-related substances. II. Effects of muscimol in monkey substantia nigra pars reticulata. J Neurophysiol 53: 292-308

Jay MF, Sparks DL (1984) Auditory receptive fields in primate superior colliculus shift with changes in eye position. Nature 309: 345-347

Judge SJ, Richmond BJ, Chu FC (1980) Implantation of magnetic search coils for measurement of eye position: An improved method. Vision Res 20: 535-538

Keller EL (1974) Participation of medial pontine reticular formation in eye movement generation in monkey. J Neurophysiol 37: 316-332

Leichnetz GR, Smith DJ, Spencer RF (1984) Cortical projections to the paramedian tegmental and basilar pons in the monkey. J Comp Neurol 228: 388-408

Leichnetz GR, Spencer RF, Hardy SGP, Astruc J (1981) The prefrontal corticotectal projection in the monkey; an anterograde and retrograde horseradish peroxidase study. Neuroscience 6: 1023-1041

Luschei ES, Fuchs AF (1972) Activity of brainstem neurons during eye movements of alert monkeys. J Neurophysiol 35: 445-461

Lynch JC, Graybiel AM, Lobeck LJ (1985) The differential projection of two cytoarchitectonic subregions of the inferior parietal lobule of macaque upon the deep layers of the superior colliculus. J Comp Neurol 235: 241-254.

Lynch JC, Mountcastle VB, Talbot WH, Yin TCT (1977) Parietal lobe mechanisms for directed visual attention. J Neurophysiol 40: 362-389

Marrocco RT, Li RH (1977) Monkey superior colliculus: properties of single cells and their afferent inputs. J Neurophysiol 40: 844-860

Mays LE, Sparks DL (1980) Dissociation of visual and saccade-related responses in superior colliculus neurons. J Neurophysiol 43: 207-232

Moors J, Vendrik AJH (1979) Responses of single units in the monkey superior colliculus to stationary flashing stimuli. Exp Brain Res 35: 333-347

Ottes FP, Van Gisbergen JAM, Eggermont JJ (1985) Latency dependence of colour-based target vs nontarget discrimination by the saccadic system. Vision Res 25: 849-862

Ottes FP, Van Gisbergen JAM, Eggermont JJ (1986) Model-based description of collicular visuomotor fields. Vision Res (submitted)

Robinson DA (1972) Eye movements evoked by collicular stimulation in the alert monkey. Vision Res 12: 1795-1808

Robinson DA, Fuchs AF (1969) Eye movements evoked by stimulation of frontal eye fields. J Neurophysiol 32: 637-648

Sandell JH, Schiller PH, Maunsell JHR (1984) The effect of superior colliculus and frontal eye field lesions on saccadic latency in the monkey. Perception 13: A6

Schiller PH (1977) The effect of superior colliculus ablation on saccades elicted by cortical stimulation. Brain Res 122: 154-156

Schiller PH, Malpeli JG (1977) Properties and tectal projections of monkey retinal ganglion cells. J Neurophysiol 40: 428-445

Schiller PH, Malpeli JG, Schein SJ (1979) Composition of geniculostriate input to superior colliculus of the rhesus monkey. J Neurophysiol 42: 1124-1133

Schiller PH, Stryker M (1972) Single-unit recording and stimulation in superior colliculus of the alert rhesus monkey. J Neurophysiol 35: 915-924

Schiller PH, Stryker M, Cynader M, Berman N (1974) Response characteristics of single cells in the monkey superior colliculus following ablation or cooling of visual cortex.

J Neurophysiol 37: 181-194
Schiller PH, True SD, Conway JL (1979) Paired stimulation of the frontal eye fields and the superior colliculus of the rhesus monkey. Brain Res 179: 162-164
Schiller PH, True SD, Conway JL (1980) Deficits in eye movements following frontal eye-field and superior colliculus ablations. J Neurophysiol 44: 1175-1189
Schnyder H, Reisine H, Hepp K, Henn V (1985) Frontal eye field projection to the paramedian pontine reticular formation traced with wheat germ agglutinin in the monkey. Brain Res 329: 151-160
Sparks DL, Holland R, Guthrie BL (1976) Size and distribution of movement fields in the monkey superior colliculus. Brain Res 113: 21-34
Sparks DL, Mays LE (1981) The role of the monkey superior colliculus in the control of saccadic eye movements: a current perspective. In: Fuchs AF, Becker W (eds) Progress in oculomotor research. Elsevier/North Holland, Amsterdam, pp 137-144
Sparks DL, Porter JD (1983) Spatial localization of saccade targets. II. Activity of superior colliculus neurons preceding compensatory saccades. J Neurophysiol 49: 64-74
Shibutani H, Sakata H, Hyvarinen J (1984) Saccade and blinking evoked by microstimulation of the posterior parietal association cortex of the monkey. Exp Brain Res 55: 1-8
Van Gisbergen JAM, Robinson DA, Gielen S (1981) A quantitative analysis of generation of saccadic eye movements by burst neurons. J Neurophysiol 45: 417-442
Van Gisbergen JAM, Van Opstal AJ, Schoenmakers JJM (1985) Experimental test of two models for the generation of oblique saccades. Exp Brain Res 57: 321-336
Wurtz RH, Albano JE (1980) Visual-motor function of the primate superior colliculus. Ann Rev Neurosci 3: 189-226
Wurtz RH, Goldberg ME (1972a) Activity of superior colliculus in behaving monkey. III. Cells discharging before eye movements. J Neurophysiol 35: 575-586
Wurtz RH, Goldberg ME (1972b) Activity of superior colliculus in behaving monkey. IV. Effects of lesions on eye movements. J. Neurophysiol 35: 587-596
Wurtz RH, Mohler CW (1976) Organization of monkey superior colliculus: enhanced visual response of superficial layer cells. J Neurophysiol 39: 745-765

GENERAL SUMMARY

This thesis describes a number of investigations into the neural mechanisms for the generation of rapid eye movements: saccades. This type of eye movement is made during a foveal scan of a static visual scene, as during the reading of this text. In a laboratory these saccades can be evoked in human subjects instructed with a visual pursuit task by a stepwise displacement of the visual target from the central fixated position towards the periphery of the retina. In a rhesus monkey, which species has a saccadic system similar as the human, single-unit activity can be recorded in cells relevant for the control of saccades. After training this animal also makes a visually guided saccade in response to the same stimulus.

To investigate the activity of nerve cells in the saccadic system, double stimuli have been used. Preceding these electrophysiological experiments behavioural studies in humans were performed to obtain insight in the response of the saccadic system to double stimuli. During the double-spot experiments (Chapter I) most (85%) trials were single spot presentations. After the central spot went off, only one peripheral spot came on. The remaining 15% of the trials were double-spot presentations, in which simultaneously two identical targets were presented at different locations within the field of view. The spatial distribution of saccade endpoints appeared to depend on the relative distance of the spot positions. For stimuli with a large difference in direction or in excentricity the response is bistable; i.e., the eye jumps either to one target or to the other. Our results show for the first time, that the response can also be bistable if the two stimuli are within one halffield. When the distance between the spots is sufficiently small averaging occurs: i.e. the saccade endpoint are distributed unimodally in between both target positions. The compromise response has been reported for double spots with a difference in eccentricity. Our data confirm this and show that the same effect also exists for stimuli with a difference in direction. These double-spot results suggest that the saccadic system has a lower spatial resolution capacity than the perceptual system, since even when the saccade response shows averaging, the targets are perceived clearly separately. The existence of cells with large receptive fields in the saccadic system, like in the SC and of cells with much smaller fields in brain areas important for visual perception, like the primary visual cortex, is interpreted as a possible neural correlate of this difference in visual resolution capacity.

In another series of behavioural experiments we applied double-spot stimuli with different peripheral spots: a green target and a red non-target spot. This is the same trial type as we used for the electro-physiological experiments in rhesus monkeys (see below). During a first series of target/non-target experiments (Chapter II) the percentage of double spots was as low as in the double-target series (about 15%). The subject, unexpectedly confronted with one of the randomly interspersed double-target presentations, often made an erroneous first saccade, not directed to the green target. Finally the eye always reaches the target, if the first saccade is wrong, one or more correction saccades are made shortly afterwards. We found, as in Chapter I, averaging for a sufficiently small distance between the spots and a bistable response for large separations. The results of the foregoing double-target experiments are, thus, not a consequence of the ambiguity in the instruction, namely to jump to one target where sometimes two are presented simultaneously.

In a second series of target/nontarget experiments (also reported in Chapter II) with 70% double-spot trials we used two different instructions, which emphasized either the speed or the accuracy of the response. A single fixed relation between the metrics of the saccade and its latency appeared to exist. Erroneous responses can only be avoided by postponing the initiation of the first saccade. These results imply that early saccades are generated reflex-like, whereas for the control of later saccades colour information is used. This is discussed in terms of a neural system consisting of two separate parallel pathways, one subcortical

and one cortical, respectively.

During our electrophysiological investigation in the generation of saccades we recorded single-unit activity in the superior colliculus (SC), because this midbrain nucleus forms a central part of the saccadic system. In this area two kind of neural activities can be measured: visual activity occurring in response to the presentation of a spot of light, and movement-related activity closely coupled to the execution of a saccade. The visual discharge only occurs if the stimulus has been presented within a limited part of the field of view: the cell's visual field. A cell with a movement-related response only fires if the ensuing saccade points to its motor field. These fields both show a gradient in the vigour of the cell discharge: it is maximal if the stimulus, or the saccade's endpoint, is in the center of the field, whereas the discharge decreases when it approaches the field's border. To determine the optimal position for a maximal cell response, we used stimulus series systematically scanning a sector of the field of view in direction and eccentricity. It is known from the literature that the retina as well as the metrics of saccades are orderly represented within a map in the SC. We proposed a quantitative model, which analytically relates the structure of this map to the shape of visuo-motor fields (Chapter III). The measured field data of SC cells were used to illustrate this new model.

In the electro-physiological measurements (see Chapter IV) we used the same target/non-target stimuli as in the behavioural studies, which were described in Chapter II. The rhesus monkey performed this colour-based discrimination task very well too. On the average about 90% of the responses to a target/nontarget stimulus consisted of a first saccade correctly pointed to the target.Our main question in this study was whether the cortical signal, on which the correct performance of the colour-discrimination task depends, reaches the saccadic system either before the SC movement-related cells (serial hypothesis) or if this system is influenced by the colour information at a lower level (parallel hypothesis). Since the movement-related discharge, during the saccadic colour-discrimination task, appears to be coupled with the saccade metrics in the same way as during a simple single spot detection task, these data corroborate the serial hypothesis. The initial sensory burst in SC cells and their 'prelude' activity, which occurs sometime before the saccade initiation, seems in some cells to be different between the presentation of a green and a red spot. Unexpectedly, in only a small fraction of the cells the prelude activity depends upon the occurrence and the metrics of the ensuing saccade. This result suggests the decision whether to make a saccade, and subsequently with which amplitude and direction is to a large extent imposed upon the SC visuomotor cells at a very late stage of saccade generation by an external source. A number of possibilities for the origin of this putative intervening signal has been indicated.

Finally, we summarize the most important results of this thesis. (1) From behavioural experiments with double-target stimuli it appears that the saccade response shows averaging if both targets are located close together and is bistable when the visual stimulus pair is presented far apart. (2) After a simultaneous presentation of a green target spot and a red non-target spot early saccades appear to be incorrect, as if under control of a colourblind system; whereas saccades initiated later in time are all target directed, which suggests that their generation has been influenced by the instruction. (3) Our model for the spatial features of the superior colliculus describes the relation between the skewness in the shape of collicular visuomotor fields, obtained by our recordings, and the non-homogenity in the structure of the retinal map in the same brain nucleus, as known from the literature. (4) From single-unit recordings in visuomotor cells in the SC of a rhesus monkey which performs a saccadic colour discrimination task, it appears that the colour information essential for a correct response reaches the saccadic system at, or above, the level of these motor cells (serial hypothesis).

ALGEMENE SAMENVATTING

Dit proefschrift beschrijft een aantal onderzoeken naar de neurale mechanismen bij de generatie van snelle sprongvormige oogbewegingen: saccaden. Dit type oogbewegingen wordt ondermeer gemaakt bij het foveaal aftasten van een stilstaand visueel beeld, zoals bij het lezen van deze tekst. In een laboratorium kunnen deze saccaden bij een, met een visuele volgtaak geïnstrueerde, proefpersoon worden uitgelokt door het visuele doel vanuit de centrale gefixeerde positie stapvormig te verplaatsen naar de periferie van de retina. Bij een rhesusaap, die een saccadisch systeem heeft dat qualitatief met dat van de mens overeenkomt, kan de activiteit worden gemeten van zenuwcellen relevant voor de sturing van saccaden. Dit proefdier maakt, na training, in responsie op dezelfde stimulus eveneens visueel geleide saccaden.

Om de activiteit van zenuwcellen in het saccadische systeem te onderzoeken werd gebruik gemaakt van dubbelstimuli. Voorafgaand aan deze elektro-physiologische experimenten werden bij de mens gedragsstudies verricht om de responsie van het saccadisch systeem op dubbel stimuli te leren kennen. In dubbeldoel experimenten (Hoofdstuk I) werden, zodra de centrale spot uitging, meestal slechts één, maar in ca 15% van de trials tegelijkertijd twee identieke doelspots op verschillende plaatsen in het gezichtsveld aangeboden. Het bleek dat de ruimtelijke verdeling van saccade eindpunten afhangt van de onderlinge afstand van de spotposities. Voor stimuli met een groot verschil in richting of in excentriciteit is de responsie bistabiel, d.w.z. het oog springt of naar het ene doel, of naar het andere. Onze resultaten tonen voor het eerst aan dat dit ook geldt indien de twee stimuli binnen een halfveld liggen. Bij een kleinere onderlinge afstand vindt middeling plaats; de saccade eindpunten liggen unimodaal verdeeld tussen de beide doelposities. Deze compromisresponsie was tot nu toe alleen gevonden voor dubbelspots met een verschil in excentriciteit. Onze experimenten bevestigen dit en tonen hetzelfde effect aan voor stimuli met een verschil in richting. Deze dubbelspot data suggereren dat het saccadisch systeem grofmaziger is dan het perceptuele systeem, want ofschoon de saccadische respons middelt, kunnen de doelen wél zeer duidelijk gescheiden worden waargenomen. Het bestaan van grote receptieve velden in cellen binnen het saccadisch systeem, zoals in de superior colliculus, en van veel kleinere velden in hersengebieden, die belangrijk zijn voor visuele perceptie, zoals de primaire visuele cortex, kan geïnterpreteerd worden als een mogelijk neuraal correlaat van dit verschil in visueel oplossend vermogen.

In een andere reeks gedragsexperimenten werden dubbelspot stimuli met twee verschillende perifere spots gebruikt: een groene doel spot en een rode niet-doel spot. Dit type trial werd ook toegepast tijdens de elektro-physiologische experimenten met rhesusapen (zie verderop). In de eerste reeks van deze doel/niet-doel experimenten (Hoofdstuk II) was het percentage dubbelspots weer laag (ca 15%). De proefpersonen, onverwachts geconfronteerd met één der in een willekeurige volgorde voorkomende dubbelspot aanbiedingen, maakten vaak een foute, niet op de groene doelspot gerichte, eerste saccade. In elk trial komt het oog uiteindelijk op het doel terecht, na een foute eerste saccade worden kort daarop een of meer correctie saccaden gemaakt. We vonden, opnieuw, middeling voor een geringe onderlinge afstand van de spots en een bistabiel gedrag voor grotere afstanden. De resultaten van de voorgaande dubbeldoel experimenten zijn dus niet een gevolg van de ambiguiteit in de instructie, nl. om een doel te volgen terwijl soms twee doelen tegelijk verschijnen.

In een tweede reeks doel/niet-doel experimenten (eveneens beschreven in Hoofdstuk II) met 70% dubbelspot trials werden twee verschillende instructies gebruikt, die óf de snelheid óf de nauwkeurigheid van de responsie benadrukten. Het bleek dat, onafhankelijk van deze instructie, er één vaste relatie tussen de metriek en de latentie van een saccade bestaat. Foute responsies kunnen alleen vermeden worden door de initiatie van saccaden uit te stellen. Deze resultaten wijzen erop dat vroege saccaden reflex-achtig worden gestuurd, terwijl bij de generatie van late saccaden kleurinformatie wordt gebruikt. Dit wordt bediscussieerd

in termen van een neuraal systeem dat bestaat uit twee gescheiden parallelle banen, respectievelijk subcorticaal en corticaal.

In ons elektro-physiologisch onderzoek naar de generatie van saccaden werd enkel-cel aktiviteit afgeleid in de Colliculus Superior (CS), omdat de cellen in deze middenhersenkern een centrale rol vervullen in het saccadisch systeem. In dit gebied vinden we zowel visuele aktiviteit, die optreedt ten gevolge van de lichtspot aanbieding, alsook bewegings-gerelateerde aktiviteit, die gekoppeld is aan het maken van een saccade. De visuele ontlading komt alleen voor na een stimulus presentatie binnen een beperkt deel van het gezichtsveld, het visuele veld. Een cel met een motorrespons vuurt alleen als de saccade gericht is naar zijn motor veld. Deze velden vertonen beide een gradient: de cel ontlading is het grootst voor een stimulus, c.q. een saccade met zijn eindpunt, in het midden van het veld, en neemt af naarmate deze dichter bij de rand ligt. Om de optimale positie voor een maximale celresponsie te vinden, gebruikten wij stimulusreeksen, die systematisch in richting en excentriciteit een sector van het gezichtsveld aftasten. Uit de literatuur is bekend dat zowel het gezichtsveld als de metriek van saccaden ordelijk gerepresenteerd ligt in een kaart binnen de CS. Een quantitatief model, dat een analytisch verband legt tussen de structuur van deze afbeelding en de vorm van de visuomotor velden, werd door ons voorgesteld (Hoofdstuk III). De gemeten veld data van CS cellen werden gebruikt om dit nieuwe model te illustreren.

Tijden de elektro-physiologische metingen (Hoofdstuk IV) werden dezelfde doel/niet-doel stimuli gebruikt als in de gedragsstudies beschreven in hoofdstuk II. Ook de rhesusaap bleek deze kleur-discriminatietaak goed uit te voeren. Onze vraagstelling was of het corticale signaal waar de correcte uitvoering van de kleurdiscriminatie taak van afhangt, het saccadisch systeem vóór de SC bewegingsgerelateerde cellen bereikt (serie hypothese) óf dat het door deze kleurinformatie pas op een lager niveau wordt beïvloedt (parallel hypothese). Omdat de bewegings gerelateerde ontlading, tijdens de saccadische kleur-discriminatie taak, op dezelfde wijze gekoppeld blijkt met de metriek van de saccade als tijdens een eenvoudige enkelspot volgtaak, ondersteunen deze data de serie hypothese. De initiele sensorische burst in SC cellen en hun prelude' aktiviteit, die enige tijd voorafgaand aan de saccade initiatie optreedt, blijkt in sommige cellen qualitatief verschillend voor de aanbieding van een groene en een rode spot. Echter slechts in een verrassend klein aantal cellen hangt de 'prelude' aktiviteit af van het optreden en de metriek van de saccade, die er op volgt. Dit resultaat suggereert dat de beslissing of, en zo ja welke saccade gemaakt moet worden in grote mate door een externe bron aan de CS wordt opgelegd. Een aantal mogelijkheden voor de oorsprong van dit beslissingssignaal wordt aangegeven.

Tenslotte vatten we de belangrijkste resultaten van dit promotie-onderzoek kort samen. 1) Uit gedragsexperimenten met dubbeldoel stimuli blijkt dat een saccadische respons middeling vertoont als beide doelen dicht bijeen liggen en bistabiel is voor een veruiteen geplaatst visueel stimuluspaar. 2) Na de gelijktijdige aanbieding van een groene doel spot en een rode niet-doel spot blijken de vroeg responsies vaak fout te zijn, alsof ze gestuurd worden door een kleurenblind systeem; terwijl later geïnitieerde saccaden allemaal doelgericht zijn, wat suggereert dat hun generatie beïnvloed wordt door instructie. (3) Ons model voor de ruimtelijke eigenschappen van de Colliculus Superior beschrijft het verband tussen de scheefheid in de vorm van de door ons gemeten colliculaire visuo-motor velden en de uit de literatuur bekende non-homogeniteit in de structuur van de retinale map in dezelfde hersenkern. (4) Uit het activiteitspatroon van visuo-motor cellen in de CS, terwijl de rhesus aap een saccadische kleur-discriminatie taak uitvoert, blijkt dat de kleurinformatie, noodzakelijk voor een correcte responsie, het saccadisch systeem op, of boven, het niveau van deze motorcellen bereikt (serie-hypothese).

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LEVENSLOOP

Op 26 juli 1952 werd ik in Amsterdam geboren. Daar heb ik mijn HBS-B opleiding aan het Van der Waalslyceum gevolgd, en deed ik in juni 1970 eindexamen. In september van datzelfde jaar begon ik mijn natuurkunde studie aan de Universiteit van Amsterdam. Na het candidaatsexamen, afgelegd in 1974, verrichtte ik mijn doctoraalstage op het Natuurkundig Laboratorium binnen de werkgroep Stralingsbeschadiging, die geleid werd door Dr M. Hermant. Het onderzoek binnen deze groep richtte zich op de migratie van puntfouten in metaal roosters. Op 13 september 1977 deed ik doctoraalexamen.

Van februari 1978 tot juni 1980 was ik als wetenschappelijk adviseur werkzaam bij de firma Optilas BV., een kleine verkooporganisatie op het gebied van lasers en optische apparatuur. Vanaf 1 juli 1980 was ik verbonden aan het Laboratorium voor Medische Fysica en Biofysica van de Universiteit van Nijmegen. Mijn onderzoek vond plaats binnen de groep Oogsturing, en werd begeleid door Dr J.A.M. van Gisbergen. Bij het samenstellen van dit proefschrift, dat de resultaten van mijn electrofysiologische studies en gedragsexperimenten aan het saccadisch oogsturingssysteem bevat, trad Prof.Dr J.J. Eggermont op als promotor.

Met ingang van 1 augustus 1985 ben ik als adviseur op het gebied van de kantoor-automatisering in dienst van het Universitair Rekencentrum, eveneens, van de Universiteit van Nijmegen.

STELLINGEN

behorende bij het proefschrift

SACCADIC EYE MOVEMENT RESPONSES TO VISUAL TARGET/NONTARGET STIMULI IN MAN AND MONKEY.

1. Ten onrechte wordt soms bij de fit van de retinotopische kaart van de primaire visuele cortex met een complex-logaritmische functie: $\vec{\omega} = B.\ln(\vec{z}+A)$ alleen de optimale waarde van vormterm A en niet van de schaalfaktor B gerapporteerd. (E.L. Schwartz, 1980, Vision Res. 20, 645-669; hoofdstuk III van dit proefschrift).

2. De z.g. vroege enhancement in visuele colliculus cellen treedt alleen op als het proefdier bij het maken van de saccade kan anticiperen op de aanbieding van de stimulus. (R.H. Wurtz, M.E. Goldberg and D.L. Robinson, 1980. In: Prog. in Physiol. Psychol. and Psychobiol.; hoofdstuk IV van dit proefschrift).

3. Het is onevenwichtig om, ter simulatie van saccadische oogsnelheid, het oogbol-oogspiersysteem te benaderen met een niet-lineaire multi-parameter vergelijking, terwijl voor de neurale innervatie een gestyleerd niet-realistisch stap-puls signaal wordt gebruikt. (A.J. Van Opstal, J.A.M. Van Gisbergen en J.J. Eggermont, 1985, Vision Res. 25, 789-801).

4. Bij elektrofysiologisch onderzoek naar de relaties tussen sensorische stimulatie, neurale aktiviteit en gedragsresponsie is het maken van een afdoend onderscheid tussen oorzaak en gevolg uiterst moeilijk.

5. Naast originaliteit en technisch/organisatorische capaciteiten voor het opzetten en uitvoeren van experimenten is redactionele vaardigheid essentieel voor een goed onderzoeker.

6. De onderwaardering van commerciele aspecten in de gezondheidszorg blijkt ook uit het ontbreken van een betaling voor de donatie van bloed.

7. Lezen bij lage lichtintensiteit is niet slecht voor de ogen.

8. Het gevoel om tot één Europa te behoren zou bij de grensbewoners van Duitsland en Nederland sterker toenemen door een versoepeling van het openbare 'kleine' grensverkeer, door b.v. de afschaffing van D-treintoeslag en IC-Zuschlag op vele van de toch steeds schaarser wordende verbindingen tussen Arnhem en Emmerich, dan door de internationale verkiezing van een Europees parlement.

9. De vermelding in het dankwoord van alle namen van degenen die aan een proefschrift hebben medegewerkt zou toegestaan moeten zijn.

10. Het verdient overweging om het aantal bij de pedel in te leveren exemplaren per proefschrift in onderling overleg vast te stellen.

11. De toenemende mate van commercialisering in overheidsinstellingen zou ook tot uitdrukking moeten komen in het door de werkgever gratis verstrekken van koffie en thee gedurende de werkpauzes, zoals dat in het bedrijfsleven gebruikelijk is.

Nijmegen, 17 oktober 1985

Fenno Ottes